MIGRANT BIRD STOPOVER ECOLOGY AND RESIDENT SPECIES LOSS IN A FRAGMENTED TROPICAL LANDSCAPE, THE SIERRA DE LOS TUXTLAS, VERACRUZ, MEXICO

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April 7, 2006

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A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

May 2006

ABSTRACT

I conducted two studies of avian ecology over the course of two spring field seasons (2003, 2004) in the Sierra de Los Tuxtlas, Veracruz, Mexico. I examined mass gains in spring Nearctic-Neotropic migrants at a stopover site near the Estacion de Biologia Tropical Los Tuxtlas. Birds were captured using mist nets. A condition index (mass/wing chord) was calculated for each individual and regressed against time of day to determine if a net gain in condition occurred at the site. Seven of 13 taxa examined showed significant gains in body condition. The average individual of none of these species carried sufficient fat to complete a trans-gulf migration from Los Tuxtlas.

Additionally, I studied the loss of resident bird species from the fragment of forest at the Biological Station. I used mist net data acquired over 8 non-breeding seasons from 1973-2004 to determine which taxa have been extirpated as the surrounding landscape became increasingly deforested. Seventeen species of birds prone to capture in mist nets have either disappeared from the station or are showing significant declines in numbers. Data indicate a continuing loss of species from the site, showing the station is not sufficient to maintain the full historic complement of birds species native to Los Tuxtlas.

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ACKNOWLEDGMENTS

The University of Alaska Museum and Friends of Ornithology provided financial support for this study. I would like to thank my advisor Dr. Kevin Winker for his support throughout the project. E. Hurtado and F. Griffiths provided field assistance. P. Escalante at the Universidad Nacional Autonoma de Mexico, Instituto de Biologia, Colleccion Nacional de Aves helped with permits and logistics. My other advisory committee members, A. Powell, and R. Barry, provided excellent advice and comments. E. Dunn provided helpful comments on Chapter 1. D. Gibson, J. Maley, E. Carr, M. Lelevier, T. Braile, C. Topp, C. Pruett, E. Humphries and particularly A. Turner offered a steady stream of support, encouragement, and comments.

General Introduction

This thesis comprises two chapters addressing the ecology and conservation of migrant and resident birds in the fragmented tropical landscape of the Sierra de Los Tuxtlas in southern Veracruz, Mexico. All field research was based out of the Estacion de Biologia Tropical Los Tuxtlas, operated by the Instituto de Ecologia at the Universidad Nacional Autonoma de Mexico. This field station protects a 700 ha tract of lowland tropical forest, one of the largest remaining forest fragments in the region. The site has been used previously for field research on migrant and resident birds, which allowed me to address questions about seasonality and faunal change over time. I re-established an array of 36 mist nets on the edge of the protected area that had been used for similar studies in the 1990s. Half of the nets were situated in primary rainforest and half in acahual (second-growth) habitat. I was able to address three questions regarding migrant birds passing through the region: What quantity of fat do migrants through this region carry? Is fat acquired during stopover? Are there differences in how this site is used for fattening between spring and autumn? Seven species were found to be depositing fat during daylight hours at the field site. A direct relationship was found between how much fat a species carried upon capture and the degree to which that taxa acquired fat. Also, a significant relationship was found between the slope of the regression lines and the percent of individuals recaptured after one night or more on the site. Species with a greater proportion recaptured showed more fattening than those with fewer recaptures. I calculated flight capacities for many of the migrant species captured at this site and found that even among those considered to be exclusively trans-gulf

migrants, the average individual carried insufficient fat reserves to complete a flight over-water from Los Tuxtlas to the southern Unites States.

Over the past fifty years the Sierra de Los Tuxtlas has lost more than 90% of its native forests. The majority of these losses have occurred in the lowlands. Deforestation and resulting fragmentation of habitat has been shown in many studies elsewhere to negatively affect the diversity of birds and organisms in the remaining fragments. No studies, thus far however, have been able to document these extirpations using a method such as mist netting, which provides sensitivity not subject to observer bias. I was fortunate to have access to mist net data from the region collected in 1973-75, 1986, and 1992-95. Using these data in addition to my own, I was able to correlate the extirpation of certain bird species from the station with deforestation and fragmentation of the surrounding landscape. Using a combination of statistical analyses and presence/absence data I was able to detect local extirpations or declines in 17 species of resident (non-migratory) birds prone to capture in mist nets. Extirpated species represent a local loss of 2.3% of the entire Los Tuxtlas avifauna, 6.3 % of the resident avifauna and 13.5% of the species captured during the study. Because large and canopy species (those not likely to be captured in mist nets) were not sampled in this study, the total number of losses is undoubtedly higher. Beyond the clear loss of habitat resulting from the deforestation, no overarching explanation for the loss of these particular species was evident. To my knowledge this is the first study to document avian species loss using a quantitative method such as mist netting.

Chapter 1: Spring stopover and fattening in migrant passerines in the Sierra de Los Tuxtlas, Veracruz, Mexico*

1.1 Abstract

The narrowing of the North American continent at the Isthmus of Tehuantepec creates the final geographic bottleneck for songbirds on their northward spring migrations. The Sierra de Los Tuxtlas, in the northwestern portion of the Isthmus, provides an ideal location from which to address questions of resource use and fat acquisition during migration. During the spring migrations of 2003 and 2004 I operated mist nets during morning and evening hours to capture passerines. Of the 13 taxa examined in this study, seven showed significant diurnal increases in body condition (an index of size-adjusted mass): Swainson's Thrush (*Catharus ustulatus*), Wood Thrush (*Hylocichla mustelina*), Magnolia Warbler (*Dendroica magnolia*), Kentucky Warbler (*Oporornis formosus*), Hooded Warbler (*Wilsonia citrina*), Worm-eating Warbler (*Helmitheros vermivorum*), and Ovenbird (*Seiurus aurocapillus*). Of these species, only the Ovenbird failed to show a significant diurnal increase in fat score. Indigo Buntings showed a significant increase in fat score but not in condition index. A comparison with autumn migration at this site indicated seasonal differences within and among species. There was no relationship between mainland vs. trans-gulf migratory strategy and increase in body condition. Results indicate a need for a reassessment of migration routes and concepts of resource use in passage.

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* Shaw, D. W. and K. Winker. Spring stopover and fattening in migrant passerines in the Sierra de Los Tuxtlas, Veracruz, Mexico. In preparation for submission to the Auk.

1.2 Introduction

Migration places intense physical demands on birds. One of the main adaptations enabling birds to make long-distance seasonal migrations is fat deposition (Blem 1990, Rogers 1991). Food resources at stopover locations are therefore critical, and, because the geography of Middle America causes a relatively rapid latitudinal decline in available space for landbirds migrating south in autumn, competition for food resources may be high. During spring migration, however, land availability for these birds increases rapidly north of the Isthmus of Tehuantepec. Several studies have addressed fattening and stopover ecology during autumn on the Isthmus and farther south in Middle America (Rogers and Odum 1966, Child 1969, Winker 1995ab, Johnson 2003), but a literature search yielded no articles regarding work conducted in spring.

My field site, located in the Sierra de Los Tuxtlas in the northwestern portion of the Isthmus of Tehuantepec, Mexico, provides an ideal location from which to study fattening strategies and stopover ecology of migrant songbirds. The ecology of migrating birds in this region is only beginning to be understood (Rappole and Warner 1980, Rappole 1995, Winker 1995ab). This site was used previously to investigate fattening in autumn migrants (Winker 1995a), which permits direct comparisons of seasonal fattening strategies. This opportunity for comparison between seasons allows a Neotropical test of the "spring fatter" hypothesis (Winker 1992, Sandberg 1996, Sandberg and Moore 1996). This hypothesis, developed for higher latitudes, suggests that migrants should carry more fat in spring than autumn due to increasing resource uncertainty in the temperate regions as migrants move north and in preparation for the impending breeding season. In

contrast, autumn migrants are departing their breeding grounds, have generally completed their prebasic molt, and are moving into regions of greater resource stability. From a tropical perspective, there should be a greater stability of resources (i.e., lower seasonality), and thus it may be hypothesized that seasonal differences as predicted by the "spring fatter" hypothesis would not be evident among passerine migrants (a group of species not known to carry fat from wintering areas to begin the breeding effort).

This study was designed to gather data on fat levels and mass gains among the common migrant passerines passing through Los Tuxtlas during spring migration. These data provide insight into seasonal and geographic patterns of fat deposition, route selection, and stopover ecology. Over the course of two spring migrations, I collected data to address the following questions: What quantity of fat do migrants through this region carry? Do migrants show a net gain in fat during stopover? Are there differences in how this site is used for fattening between spring and autumn?

1.3 Study area and methods

1.3.1 Study area

I conducted fieldwork in the Sierra de Los Tuxtlas, located in southern Veracruz, Mexico, 90 km southeast of Veracruz city (Fig. 1.1). This range of mountains lies in the northwestern portion of the Isthmus of Tehuantepec and is isolated from the Sierra Madre Oriental by extensive lowlands. The Los Tuxtlas region encompasses approximately 42,000 km^2 and is dominated by Volcan San Martin and Volcan Santa Marta, each reaching more than 1,500 m in elevation. The Gulf of Mexico lies a short distance from the mountains to the north and east. Habitat in the region was formerly dominated by the

farthest north Neotropical evergreen rainforest, but due to deforestation is now a mosaic with a high percentage of pastureland, fencerows, and isolated trees (Dirzo and Garcia 1992). Andrle (1966) estimated that 50% of the region was forested in 1962; by 1986 15% of forests remained (Winker et al. 1990, Dirzo and Garcia 1992), and in 1994 only 7-10% of the region was forested (Winker 1997). Remaining forest lies primarily in the highlands, and is scarce below 500 m above sea level (Rappole et al. 1994).

The field site lies on the southern edge of the 700 ha Estacion de Biologia Los Tuxtlas (18° 34'30"N, 95° 04'20"W), operated by the Instituto de Biologia at the Universidad Nacional Autonoma de Mexico. The field station protects one of the few remaining large tracts of lowland evergreen forest in the region. The climate is hot and wet, with a mean annual temperature of 25° C (Soto and Gama 1997). Annual precipitation is 4.5-4.9 m, with a short dry season from March-May (Soto and Gama 1997). My netting site was on the edge of the Estacion in primary and second-growth forests approximately 150 m above sea level. The exact netting site was used previously by Winker (1995a). Canopy heights in the primary forest ranged from 30-35 m (Ibarra-Manriquez et. al. 1997). Second growth areas had variable canopy heights from 3-20 m (pers. obs.).

1.3.2 Field methods

Thirty-six standard nylon mist nets (12 x 2.6 m, 30 and 36 mm mesh) were placed in primary and second-growth forest, and operated (weather permitting) during daylight hours. Effort was concentrated in the morning and evening hours. Between 21 February and 27 April 2003 nets were open for 8,395 net hrs and from 5 to 29 April 2004 for 2,312

net hrs. I placed captured birds in light cloth bags and brought them to a central processing area. Birds were banded, wing chord and tail lengths were measured to the nearest 0.1 mm using vernier calipers, and birds were then weighed to the nearest 0.1 g using Pesola spring scales. Fat scores were assigned following Helms and Drury (1960). I collected a small number of birds to examine stomach contents and to prepare as museum specimens following Winker (2000).

1.3.3 Data analyses

T-tests were used to test for gross differences in overall condition (mass/wing chord x 100) between years. I pooled data from both field seasons because only Hooded Warbler (*Wilsonia citrina*) showed a significant difference between years ($t = 1.99$, $P = 0.013$). To avoid confounding analyses for the Hooded Warbler with apparent between-year differences, I selected 2003 for analyses for that species due to the larger sample for that year (2003:171 vs. 2004:36). Twelve migrant species and the genus *Empidonax* had sufficient numbers of captures for analyses (e.g., $N \geq 30$; Table 1.1). In addition, I pooled data for Least Flycatcher (*Empidonax minimus*) and "Traill's" Flycatchers (*E. alnorum* and *E. traillii*) to make the sample size for *Empidonax* flycatchers sufficient for analyses.

Birds foraging in a suitable environment should show a diurnal increase in mass due to food intake and fat deposition with subsequent loss at night due to fasting, nocturnal metabolism and excretion of undigestible material. Non-foraging individuals, or those in an unsuitable environment, should show a diel or 24 h decrease in mass. I created a "condition index" for each first-time capture by dividing mass by wing chord and multiplying by a constant (100). Wing chord has been shown elsewhere to be an

appropriate proxy for size (Winker 1992, 1995a, Johnson 2003). The inclusion of a size-related variable in this index somewhat corrected for size differences among individuals. This technique of mass-gain analysis was originally presented by Winker (1992) and modified by Winker (1995a), which examined species-level trends. Body mass, due to its quantitative nature, is the most important variable. Mass has been shown in fat-free mass studies to correlate with fat carried (Rogers 1965, Rogers and Odum 1966). The underlying assumption of this measure of condition was that this size-corrected index is correlated with the amount of fat carried.

Fat scores are somewhat qualitative and subject to variation between observers and are thus not suitable for use in the preceding method of analysis. However, gauging fat content based on visible furcular and abdominal fat, though qualitative, and subject to observer variation may provide corroborative evidence for trends observed in condition indices (Dunn 2002). Due to the categorical nature of fat scores standard linear regressions may not be appropriate, however such analyses have been used in other studies (e.g. Dunn 2001, 2002, Johnson 2003) and are therefore presented here for comparative purposes. To determine if using an ordinal regression would yield different results I conducted both linear and ordinal regression for these data. I regressed fat scores on time of day of capture using both methods.

To determine diurnal mass gains, I took the slope of the regression line for trends in condition index (if significantly different from zero) and multiplied it by the average number of hours of bird activity (12.5 h from field notes), then multiplied by the sample's average wing chord. Mass used alone without incorporating a size related variable does

not account for individual variation, which can be substantial in songbirds (Winker 1992). In a location where most individuals do not remain on the site for more than 24 h, recaptures may not be representative of the entire population and were therefore excluded for regression analyses (Winker 1992). Total 24 h mass gains were estimated by subtracting nocturnal loss (estimated as 4.5% of average body mass from Mueller and Berger 1966) from the diurnal increase.

To determine if species carrying a higher proportion of fat acquire less fat than those with relatively low reserves I conducted a regression of the estimate of percent of mass gained in a 24 h period against percent of mass greater than the fat free mass (from Odum in Dunning 1993) for the species that showed significant diel gains. Linear regression was selected for this analysis due to the apparent linear nature of the data.

Percents of species recaptured after a night or more at the site were regressed against slopes of the condition index regression to determine if a relationship between time on the site and fattening was present.

The number of hours and distance that the average captured individual was capable of flying were estimated using the average species-level diel gains, rates of energy use during migration (Tucker 1974), and published values for the energetic content of fat and flight speed (39.8 kJ/g and 40.7 km/h, Nisbet et al. 1963). Additionally, I calculated the proportion of the population capable of making the flight from the Sierra de Los Tuxtlas across the Gulf of Mexico in a single flight.

1.4 Results

Swainson's Thrushes (*Catharus ustulatus*), Wood Thrushes (*Hylocichla mustelina*), Hooded, Magnolia, and Kentucky warblers (*Wilsonia citrina, Dendroica magnolia,* and *Oporornis formosus*), and Ovenbirds (*Seiurus aurocapillus*) showed significant positive slopes in condition index (Table 1.2, example in Fig. 1.2). No species showed negative nonzero slopes. Diurnal condition slopes did not differ significantly from zero in six taxa: the genus *Empidonax,* Gray-cheeked Thrushes (*Catharus minimus*), Gray Catbirds (*Dumetella carolinensis*), Worm-eating Warblers (*Helmitheros vermivorum*), Yellow-breasted Chats (*Icteria virens*), and Painted and Indigo buntings (*Passerina ciris* and *P. cyanea*).

Both linear and ordinal regressions of fat scores on time of day indicated the same species showed significant gains. These results generally corroborated the observed increases in condition index. Of the study species showing significant diurnal gains in condition, only the Ovenbird failed to show corresponding significant diurnal increases in fat score. The Indigo Bunting, although not displaying positive gains in condition index, showed a significant increase in fat score (Table 1.2).

Diurnal gains in mass were estimated for those seven species with trends in condition index that were significantly different from zero. Subtracting the estimated nocturnal loss gave an estimate of average mass gain over a 24 h period. Degree of mass gained varied from 2.8-7.7% of a species' average body mass (Table 1.3). No species showed a net loss in condition, as was observed on the site during autumn (Winker

1995a, Johnson 2003). Estimated gains were lowest in Swainson's Thrush (2.8%) and highest in Wood Thrush (7.7%; Table 1.3).

Body molt was evident in several species, with a considerable percentage of Indigo Buntings (34%), Magnolia Warblers (34%), and *Empidonax* flycatchers (36%) showing some degree of feather growth. This added energetic demand may limit the amount of fat that individuals can carry and their ability to fatten. Of these three species, Magnolia Warblers showed a significant positive increase in both body condition and fat score through the day, and Indigo Buntings had significant positive diel gains in fat score.

Winker (1995a) found that some species showed a relationship between wing chord and time of day of capture, which might confound results. For data collected during this study, I found no significant relationships between time of capture and wing chord for any species examined.

Nine of the ten species for which there were published data on fat-free mass (mean, sample size, minimum-maximum, standard deviation) (Odum in Dunning 1993) were significantly heavier than fat-free mass (Table 1.4). Only Magnolia Warblers were not significantly different. However the lack of visible fat does not preclude the presence of internal or blood-borne fat, (extracted in Odum in Dunning 1993) and fat-scoring is subject to variation (Krementz and Pendleton 1990; Table 1.5). Nevertheless, use of fat-free estimates based on fat scores provides a second useful method for estimating the amount of fat available for migration, and results are included here for comparison.

To document that individuals of the study species were in fact foraging on the site I examined stomach contents for collected individuals. Every individual collected of the

study species had food in the stomach (Table 1.6). Fruit dominated the stomach contents of the thrushes and buntings, and invertebrates were most abundant in the warblers and flycatchers. This corroborated observations of birds foraging on the site during netting hours (pers. obs.).

Study individuals and species differ in migration distance from Los Tuxtlas. Over the full course of the migration the total consumption and need of resources for migration will be greater for those covering larger distances. However, whether long-distance migrants require significantly more resources than short-distance migrants at any given stopover location is uncertain. If differences exist, species such as Swainson's and Gray-cheeked thrushes, which are long-distance migrants, should fatten more than short-distance migrants such as Painted Buntings and Hooded Warblers. To determine whether migration distance affected fattening strategy at this site, I used linear regression to compare the slope of the line from the condition index regression for the 13 study species against the distance to the middle of the species' breeding range. Distances were estimated using range maps in the Birds of North America series (Payne 1992, Briskie 1994, Evans-Ogden and Stutchberry 1994, Hall 1994, VanHorn and Donovan 1994, Cimprich and Moore 1995, Roth et al. 1996, Hanners and Patton 1998, McDonald 1998, Lowther et al. 1999, Evans-Mack and Yong 2000, Sedgwick 2000, Eckerle and Thompson 2001, Lowther et al. 2001). I found no relationship between migration distance from Los Tuxtlas and fattening ($F = 0.271$, $P = 0.62$).

When testing whether the degree of fattening observed was affected by the total amount carried on average I found a significant negative correlation for the seven species

showing significant diel gains ($F = 10.38$, $P = 0.023$; Fig. 1.3). Additionally, when the percent of recaptures was regressed against the slopes of the condition index regressions for all study species a significant relationship was found ($r^2 = 0.399$, $F = 7.289$, $P = 0.021$). This finding indicates that species with a higher proportion of individuals spending more than one day on the site fatten more than those remaining only a single day (Table 1.7).

Flight capacities were estimated for those species for which fat-free mass data were available. Based on daily net gains for those species showing significant fattening (Table 1.3), the average individual of these species was capable of between 3 and 8 hours of flight after a single day's foraging (Table 1.8). Total flight distances, assuming still air and exhaustion of all fat reserves (assuming all mass above fat-free mass is fat), would allow a range of from 300 to 960 km, depending on species (Table 1.8). These distances are insufficient for a trans-gulf flight of 1150 km departing from Los Tuxtlas to the southern United States. Using the technique of basing flight capacity estimates on the average mass of individuals with zero fat score, these distances are substantially reduced, from 87 to 557 km, as are the number of individuals capable of completing a trans-gulf flight (Table 1.9). The average mass of Gray-cheeked Thrushes with zero fat score, perhaps due to geographic variation in body size or unknown factors, was 0.7 g less than the fat-free mass presented in Odum (in Dunning 1993), and the estimated flight capacity presented in Table 1.8 for that species is therefore appreciably greater than in Table 1.6. For all other species, the average mass of individuals with fat scores of zero was greater than the fat-free mass.

To determine the proportion of the sample population capable of completing a trans-gulf flight, I calculated the amount of fat necessary for each species using both of the above techniques for estimating fat content, and compared it to the estimated amount of fat carried by each individual (Table 1.9). Percentages of the populations of study species capable of the flight varied from 2.6% to 42.7% using a base of fat-free mass data (Odum in Dunning 1993; e.g., Fig. 1.4) and from 0% to 16.7% using a base of zero-fat score individuals. Hooded Warblers showed a dramatic difference between the two techniques (42.7% vs. 0%), while some species varied little.

1.5 Discussion

The majority of migrant passerines moving through Los Tuxtlas are carrying substantial quantities of fat. Nine of the ten study species that were comparable with Odum (in Dunning 1993) had an average body mass significantly greater than fat-free mass. Percentages showed wide variation from 7-23% of live mass as fat. This amounts to substantial energetic reserves, particularly for those species at the higher end of this range. However, as demonstrated (Tables 1.5, 1.8), neither diel gain no total fat carried was sufficient for the average individual of any species to cross the Gulf of Mexico from Los Tuxtlas.

Of the thirteen study taxa, eight showed significant diel gains in either body condition or fat score. Although lack of power due to small sample sizes may account for some of the interspecific variation in the apparent presence or absence of gains in fat or condition, it cannot fully explain why some but not all taxa showed significant gains. Species such as Yellow-breasted Chat and Gray-cheeked Thrush did not show any

indication of change in diurnal condition or fat score trends despite substantial sample sizes (Tables 1.1 and 1.2).

Sandberg (1996), and Sandberg and Moore (1996) hypothesized that resource uncertainty and the impending breeding season would cause spring migrants to fatten more dramatically during migration through more northern latitudes than in autumn, and Winker (1995a) proposed the same pattern might be found at the Los Tuxtlas site. However, the percentage of species showing significant fattening was not different between seasons at this site (6 of 11 species [55%] in Winker (1995a), and 7 of 13 species [54%] in this study). Diel gain, determined by meeting identical assumptions as Winker (1995a), was substantially lower in this study, despite comparable slopes. Among species showing gains, an average of 5% of body mass was acquired during a hypothetical 24 h period, whereas Winker (1995a) detected a 13% average increase in autumn for the same period. When all study species are included, average gains decline in Winker (1995a) to 4.4% and in this study to 2.7%. Species showing significant gains also differed between seasons.

Molt was noted in three taxa. Two of the three showed significant diel gains either in condition index or fat score. Although molt undoubtedly places an additional energetic demand on migrating birds, it does not appear to prevent a net gain in fat at this site.

Migration strategies differ among species; some of the study species are categorized as exclusively trans-gulf migrants, others follow the coast northward, and a few use both routes (Payne 1992, Briskie 1994, Evans-Ogden and Stutchbury 1994, Hall

1994, Van Horn and Donovan 1994, Cimprich and Moore 1995, Roth et al. 1996, Hanners and Patton 1998, McDonald 1998, Lowther et al. 1999, Evans-Mack and Yong 2000, Sedgwick 2000, Eckerle and Thompson 2001, Lowther et al. 2001; Table 1.2). Migrants at this site are carrying insufficient fat for long distance flight; therefore, exclusively trans-gulf migrants might be expected to demonstrate higher levels of fattening, or remain longer at the site to accomplish a long overwater flight. If trans-gulf migrants demonstrate higher levels of fattening then Gray-cheeked Thrushes, Magnolia, Hooded and Worm-eating warblers, Ovenbirds, and Indigo Buntings should show a strong tendency to fatten. In addition to those known to migrate exclusively over the gulf, several species (Swainson's Thrushes, Wood Thrushes, Gray Catbirds, Yellow-breasted Chats, and Painted Buntings) migrate over the Gulf of Mexico or along the coast. For this group, the site could serve as a departing point for trans-gulf migrations or as a stopover on the coastal route, and fattening strategy could vary among individuals. Strictly landbound migrants (e.g., any of these species) would seem to have little need to acquire large quantities of fat, and thus trends in fattening are expected to be less distinct. Variability should be less in the species using a single migration route as opposed to those species that separate their migration into either trans-gulf or coastal routes. However, an ANOVA comparing the standard errors of the regressions of single route migrants to that of dual-route migrants failed to show significant differences between groups ($F = 0.144$, $P = 0.932$)

If the estimates made here are correct, there is a tendency for birds to fatten less dramatically in spring at this site than in fall. This is similar to findings by Benson and

Winker (2005) in central Alaska. At their site in Alaska they found higher fat loads among birds departing the breeding grounds in autumn than among those arriving in spring. However, at Los Tuxtlas in autumn, Winker (1995a) detected no significant diel condition increases in Wood Thrushes, Hooded Warblers, and Ovenbirds, each of which showed significant increases at the same site during spring. All three of these species winter in large numbers in Los Tuxtlas and surrounding regions. It is likely that many individuals captured in autumn were arriving on or near their wintering grounds and had no need to fatten. In spring, these species are embarking on migration and/or arriving from areas to the south, and the need for fattening may be greater. However, Gray Catbirds also winter in Los Tuxtlas, and Winker (1995a) detected significant diel gains in this species where none were apparent in spring.

If a direct overwater route is followed from Los Tuxtlas by any of these species, two possible destinations are Galveston, Texas and Mobile, Alabama, 1,150 km and 1,500 km from the Sierra de Los Tuxtlas, respectively. My calculations based on Tucker (1974) and Nisbet et al. (1963), indicate that individuals of the study species vary in the distances they are capable of flying from the site. For no taxa did the average individual carry sufficient fat reserves for a single trans-gulf flight (Tables 1.8 and 1.9). No greater proportion of the populations of trans-gulf migrants were capable of making a trans-gulf flight than taxa with coastal or dual migration strategies (Table 1.9, Fig. 1.4). This provides strong inference that birds were generally not crossing the Gulf of Mexico directly from the Isthmus of Tehuantepec on the night of capture. Notably, all these estimates are working under the assumption of calm wind conditions across the Gulf of

Mexico. If a tail wind was present, aiding the birds on their northward flight, the proportion of the populations of migrant species capable of the flight might increase substantially.

Winker (1995a) proposed that during autumn the majority of his captures were not birds arriving from a trans-gulf flight, but were likely birds moving south down the coast to arrive in Los Tuxtlas. During spring, birds from my field site were likely reversing Winker's (1995a) proposed route and following the coast northward before making shorter overwater crossings of the northern gulf or avoiding overwater flights altogether. Of my 13 study taxa, 11 were noted in Rappole et al's (1979) study of a stopover site in southern Texas. In addition they found significant numbers of individuals of my study species at that site during spring migration. This may indicate that some individuals of species thought to be exclusively trans-gulf migrants are in fact moving northward by way of the Gulf coast and crossing few areas or only short distances over open water. Another possibility is that species from Los Tuxtlas known as exclusively trans-gulf migrants are moving eastward along the southern coast of the Gulf of Mexico then making the crossing by way of the Yucatan Peninsula. Both of these explanations allow for the arrival of migrants at observation points in the southeastern United States either by land or water (Stevenson 1957, Gauthreaux 1971, Rappole et al. 1979, Yong and Moore 1997). Sampling migrant abundance along the gulf coast from the Isthmus northward would provide valuable information about departure and arrival points for trans-gulf migrants. If routes and distances fail to explain variation among species either within or between seasons, another simple hypothesis proposed by Dunn

(2001) may apply. She proposed that birds arriving at a stopover location with sufficient resources need only a place to rest and maintain their energetic reserves, and they may not show substantial net gains even in ideal habitat. The significant negative relationship found here (Fig. 1.3) between a species-level estimate of fat levels and the amount of fat a species gained (on average) in a day at this site suggests that this simple relationship may scale up to the species level and help explain single-site patterns among species. I also tested a second simple explanation. Species that tend to spend a greater amount of time on the site are also likely to show more fattening than those remaining only a few hours (Table 1.7). I found a significant positive correlation. These two simple explanations may provide insight into single-site patterns of fattening better than routes, distances traveled, or even seasonality through a complete migration cycle.

It is clear that current assumptions regarding migration routes, distances, and passerine energetics are insufficient to explain the findings of this research. Species thought to be exclusively trans-gulf migrants were, on average, carrying insufficient resources to accomplish a gulf crossing from Los Tuxtlas. The greater demands that have been hypothesized at higher latitudes for spring migrants do not translate into heavier spring fattening at this Neotropical site. Previously published hypotheses regarding seasonal fattening strategies in passerine migrants do not seem to apply to spring Middle American migrants. It appears that simple explanations such as total amount of fat carried and time spent on the site best predict the degree of fattening to occur at this site. Though we may develop reasonable explanations for the patterns of fattening observed

on this site, the puzzle of passerine migration as a whole does not appear to conform to broad, generalized explanations.

1.6 Literature Cited

Andrle, R. F. 1964. A biogeographical investigation of the Sierra de Tuxtla in Veracruz, Mexico. Ph.D. dissertation. Louisiana State University, Baton Rouge.

Benson, A. M., and K. Winker. 2005. Fat deposition strategies among high-latitude passerine migrants. Auk 122:544-557.

Blem, C. R. 1990. Avian energy storage. Current Ornithology 7:59-113.

Briskie, J. V. 1994. Least Flycatcher (Empidonax minimus). In The Birds of North America, No. 99 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Child, G. I. 1969. A study of nonfat weights in migrating Swainson's Thrushes (*Hylocichla ustulata*). Auk 86:327-388.

Cimprich, D. A., and F. R. Moore. 1995. Gray Catbird (*Dumetella carolinensis*). In The Birds of North America, No. 167 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Dirzo, R., and M. C. Garcia. 1992. Rates of deforestation in Los Tuxtlas, a neotropical area in southeast Mexico. Conservation Biology 6:84-90.

Dunn, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72:419-432.

Dunn, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin 114:368-379.

Dunning, J. B., Jr. 1993. CRC handbood of avian body masses. CRC Press, Boca Raton, Florida.

Eckerle, K. P., and C. F. Thompson. 2001. Yellow-breasted Chat (*Icteria virens*). In The Birds of North America, No. 575 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Evans Mack, D., and W. Yong. 2000. Swainson's Thrush (*Catharus ustulatus*). In The Birds of North America, No. 540 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Evans Ogden, L. J., and B. J. Stutchbury. 1994. Hooded Warbler (*Wilsonia citrina*). In The Birds of North America, No. 110 (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Gauthereaux, S. A., Jr. 1971. A radar and direct visual study of passerine spring migration in southern Lousiana. Auk 88:343-365.

Hall, G. A. 1994. Magnolia Warbler (*Dendroica magnolia*). In The Birds of North America, No. 136 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Hanners, L. A., and S. R. Patton. 1998. Worm-eating Warbler (*Helmitheros vermivorus*). In The Birds of North America, No. 367 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Helms, C. W., and W. H. Drury. 1960. Winter and migratory weight and fat field studies of some North American buntings. Bird Banding 31:1-40.

Ibarra-Manriquez, G., M. Martinez-Raomos, R. Eirzo, and J. Nunez-Farfan. 1997. La vegetacion. *In* E. Gonzalez-Soriano, R. Dirzo and R.C. Vogt (eds.), Historia natural de Los Tuxtlas. Universidad Nacional Autonoma de Mexico, Mexico, D.F., Mexico. Pg. 61-174.

Johnson, A.B. 2003. Migrant stopover ecology and resident resilience after hurricane Iris in a neotropical bird community. M.S Thesis. University of Alaska Fairbanks.

Krementz, D.G., and G.W. Pendleton. 1990. Fat scoring: sources of variability. Condor 92:500-507.

Lowther, P. E., S. M. Lanyon, and C. W. Thompson. 1999. Painted Bunting (*Passerina ciris*). In The Birds of North America, No. 398 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Lowther, P. E., C. C. Rimmer, B. Kessel, S. L. Johnson, and W. G. Ellison. 2001. Gray-cheeked Thrush (*Catharus minimus*). In The Birds of North America, No. 591 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Payne, R. B. 1992. Indigo Bunting (*Passerina cyanea*). In The Birds of North America, No. 4 (A. Poole, Peter Stettenheim, and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, DC; The American Ornithologists' Union.

McDonald, M. V. 1998. Kentucky Warbler (*Oporornis formosus*). In The Birds of North America, No. 324 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Mueller, H. C., and D. D. Berger. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. Bird Banding 37:83-112

Nisbet, I. C. T., W. H. Drury, Jr., and J. Baird. 1963. Weight loss during migration. Part I. Deposition and consumption of fat by the Blackpoll Warbler. Bird-Banding 34:107-159.

Rappole J.H., Ramos M.A., Oehlenschlager R.J., Warner D.W., and Barkan C.P. 1979. Timing of migration and route selection in North American songbirds. Pages 199-214 in L. Drawe, editor. Proceedings of the First Welder Wildlife Foundation Symposium. Sinton (TX): Welder Wildlife Foundation.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353-393 in A. Keast and E.S. Morton, editors. Migrant birds in the Neotropics. Smithsonian Institution Press, Washington D.C.

Rappole, J. H., G. V. N. Powell, and S.A. Sader. 1994. Remote sensing of tropical habitat availability for a nearctic migrant: the Wood Thrush. Pages 91-104 in R. Miller , editor. Use of remote sensing in conservation. Chapman Hall, New York.

Rappole J. H. 1995. The ecology of migrant birds: a Neotropical perspective. Smithsonian Institution Press, Washington D.C.

Rogers, D. T., Jr. 1965. Fat levels and estimated flight-ranges of some autumn migratory birds killed in Panama during a nocturnal rainstorm. Bird-Banding 36:115-116.

Rogers, C. M. 1991. An evaluation of the method of estimating body fat by quantifying visible subcutaneous fat. Journal of Field Ornithology 62:349-356.

Rogers, D. T., and E. P. Odum. 1966. A study of autumnal postmigrant weights and vernal fatting of North American migrants in the tropics. Wilson Bulletin 78:415-433.

Roth, R. R., M. S. Johnson, and T. J. Underwood. 1996. Wood Thrush (*Hylocichla mustelina*). In The Birds of North America, No. 246 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

Sandberg, R. 1996. Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. Ibis 138:514-524.

Sandberg, R., and F. R. Moore. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. Oikos 73:577-581.

Sedgwick, J. A. 2000. Willow Flycatcher (*Empidonax traillii*). In The Birds of North America, No. 533 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Soto, M., and L. Gama. 1997. Climas. In E. Gonzalez-Soriano. R. Dirzo and R.C. Vogt (eds.) Historia Natural de Los Tuxtlas. P. 7-23. Universidad Nacional Autonoma de Mexico, Mexico, D.F., Mexico.

Stevenson, H. M. 1957. The relative magnitude of the trans-gulf and circum-gulf spring migrations. Wilson Bulletin 69: 39-77.

Tucker, V. A. 1974. Energetics of natural avian flight. Publications of the Nuttall Ornithological Club 15:298-333

Van Horn, M. A., and T. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). In The Birds of North America, No. 88 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Winker, K., J. H. Rappole, and M. A. Ramos. 1990. Population dynamics of the Wood Thrush in southern Veracruz, Mexico. Condor 92:444-460.

Winker, K., D. W. Warner, and A. R. Weisbrod. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:953-862.

Winker, K. 1995a. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropic migrants. Auk 112:690-700.

Winker, K. 1995b. Neotropical stopover sites and Middle American migrations: The view from southern Mexico, p. 150-163. *In* M. Wilson and S. Sader, [Eds.] Conservation of Neotropical migratory birds in Mexico. Maine Agricultural and Forest. Experiment Station Miscellaneous Publication, Orono, Maine.

Winker, K. 1997. Introducción a las aves de Los Tuxtlas. p. 535-543. *In* E. González S., R. Dirzo, and R. Vogt, eds. Historia Natural de Los Tuxtlas.

Winker, K. 2000. Obtaining, preserving and preparing bird specimens. Journal of Field Ornithology. 71(2): 250-297.

Yong, W., and F. Moore. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263-278.

Table 1.1. Sample sizes and quantified variables (mean ± standard deviation) for 13 taxa captured during spring of 2003 and 2004 (Hooded Warbler 2003 only) at the Sierra de Los Tuxtlas, Mexico.

Species	*n*	Mass	Wing chord	Tail	Fat score
Empidonax sp.	35	11.8 (4.91)	66.5 (7.75)	55.5 (5.07)	0.8 (0.9)
Gray-cheeked Thrush (*Catharus minimus*)	58	27.1 (3.14)	98.8 (3.78)	69.1 (4.52)	1.4 (0.9)
Swainson's Thrush (*Catharus ustulatus*)	323	30.8 (3.40)	95.5 (5.68)	66.2 (3.52)	2.1 (1.2)
Wood Thrush (*Hylocichla mustelina*)	120	47.6 (5.99)	100.0 (14.73)	67.6 (3.39)	2.1 (1.5)
Gray Catbird (*Dumetella carolinensis*)	38	35.1 (2.62)	86.9 (2.65)	89.8 (3.83)	1.3 (1.1)
Magnolia Warbler (*Dendroica magnolia*)	39	7.9 (0.83)	57.5 (2.07)	47.2 (2.11)	0.9 (1.0)
Kentucky Warbler (*Oporornis formosus*)	136	13.4 (1.67)	65.0 (2.60)	46.8 (2.41)	1.7 (1.4)
Hooded Warbler (*Wilsonia citrina*)	171	11.0 (2.93)	61.9 (3.98)	53.8 (4.23)	1.8 (1.3)
Worm-eating Warbler (*Helmitheros vermivorum*)	78	13.7 (1.82)	66.7 (2.91)	47.7 (2.36)	2.5 (1.6)
Yellow-breasted Chat (*Icteria virens*)	43	26.4 (2.81)	73.6 (2.53)	71.4 (3.76)	2.4 (1.3)
Ovenbird (*Seiurus aurocapillus*)	68	18.5 (1.81)	72.7 (2.62)	51.6 (1.83)	1.3 (1.1)
Painted Bunting (*Passerina ciris*)	31	15.8 (1.89)	69.4 (2.67)	53.8 (2.46)	1.4 (1.3)
Indigo Bunting (*Passerina cyanea*)	159	15.2 (4.57)	65.7 (4.94)	50.0 (3.39)	1.4 (1.2)

Table 1.2. Regression results for fat score (1) and condition index (2) on time of capture and migration strategy for 13 taxa captured during spring migration at the Sierra de Los Tuxtlas, Mexico.

	Condition Index			Fat Score			Migration
Species	r^2	*F*	*P*	r^2	*F*	*P*	strategy
Empidonax sp.	0.071	2.36	ns	0.076	2.53	ns	mainland
Gray-cheeked Thrush	0.005	0.28	ns	0.003	0.16	ns	trans-gulf
Swainson's Thrush	0.038	12.10	<0.001	0.069	24.37	<0.001	mainland and gulf
Wood Thrush	0.088	11.06	<0.001	0.067	8.16	0.005	mainland and gulf
Gray Catbird	0.003	0.09	ns	0.011	0.40	ns	mainland and gulf
Magnolia Warbler	0.130	5.39	0.026	0.163	7.03	0.012	trans-gulf
Kentucky Warbler	0.048	6.59	0.011	0.065	8.98	0.003	mainland

Table 1.2. (continued)

Species	Condition Index			Fat Score			Migration strategy
	r^2	F	P	r^2	F	P	
Hooded Warbler	0.063	11.33	<0.001	0.160	31.94	<0.001	trans-gulf
Worm-eating Warbler	0.058	4.62	0.035	0.066	5.27	0.025	trans-gulf
Yellow-breasted Chat	0.007	0.31	ns	0.011	0.44	ns	mainland and gulf
Ovenbird	0.057	4.01	0.049	0.037	2.48	ns	trans-gulf
Painted Bunting	0.002	0.05	ns	0.014	0.42	ns	mainland and gulf
Indigo Bunting	0.009	1.34	ns	0.063	10.31	0.002	trans-gulf

Table 1.3. Summary of linear model for change in mass, indicating slope (m), diurnal gain (g) based on a 12.5 h day, nocturnal loss (g) based on 4.5% of species' mean mass, estimated 24 h net gain (g), and what this gain represents in percentage of the species' average mass at the Sierra de Los Tuxtlas in spring.

Species	*m*	Diurnal gain	Nocturnal loss	Net gain/day	% of mass
Swainson's Thrush	0.00188	2.243	1.386	0.858	2.79
Wood Thrush	0.00465	5.813	2.141	3.671	7.72
Magnolia Warbler	0.00146	1.046	0.411	0.634	6.94
Kentucky Warbler	0.00171	1.393	0.601	0.791	5.92
Hooded Warbler	0.00118	0.913	0.488	0.424	3.91
Worm-eating Warbler	0.00150	1.253	0.615	0.638	4.67
Ovenbird	0.00156	1.418	0.831	0.587	3.18

Table 1.4. Comparison of fat-free mass (from Odum in Dunning 1993) to mean mass of study species captured in spring at the Sierra de Los Tuxtlas using two-sample *t*-tests.

Species	Fat Free Mass (g)	Tuxtlas Mass (g)	Difference (g)	% of Live Mass	*t*	*P*
Gray-cheeked Thrush	25.20	27.13	1.93	7	3.78	<0.001
Swainson's Thrush	24.18	30.79	6.61	21	28.89	<0.001
Wood Thrush	42.21	47.54	5.33	11	8.37	<0.001
Gray Catbird	31.80	35.09	3.29	9	6.94	<0.001
Magnolia Warbler	6.92	7.89	0.97	12	0.75	ns
Kentucky Warbler	11.36	13.38	2.02	15	13.61	<0.001
Hooded Warbler	8.20	10.60	2.40	23	22.63	<0.001
Worm-eating Warbler	10.79	13.62	2.83	21	12.08	<0.001
Ovenbird	15.52	18.55	3.03	16	10.87	<0.001
Indigo Bunting	12.34	14.70	2.36	16	14.58	<0.001

Table 1.5. Flight capacity estimates based on birds captured at Los Tuxtlas presenting mean, sample sizes and standard deviations, estimated fat, and maximum hours and distances possible assuming all mass greater than the average when fat score is zero is fat that could be used for migration.

Species	Tuxtlas zero fat score (N,SD)	Estimated Fat (g)	Maximum hours of flight	Maximum flight distance (km)
Empidonax sp.	10.81 (12, 1.09)	1.02	9.02	367
Gray-cheeked Thrush	24.50 (5, 2.81)	2.63	10.36	422
Swainson's Thrush	26.84 (16, 2.13)	3.95	13.76	560
Wood Thrush	42.29 (13, 4.81)	5.25	11.98	488
Gray Catbird	34.39 (7, 2.70)	0.70	2.15	87
Magnolia Warbler	7.64 (7, 0.85)	0.34	4.46	182
Kentucky Warbler	11.99 (37, 0.85)	1.39	10.90	444
Hooded Warbler	9.52 (28, 0.68)	1.08	10.63	434
Worm-eating Warbler	11.86 (8, 1.00)	1.76	13.57	552
Yellow-breasted Chat	23.00 (1, na)	3.38	13.69	557
Ovenbird	17.59 (21, 2.09)	0.96	5.48	223
Painted Bunting	15.44 (4, 0.71)	0.37	2.47	100
Indigo Bunting	13.66 (33, 1.24)	1.51	10.48	427

Table 1.6. Sample sizes for stomach content examinations.

Species	*n*
Empidonax minimus	4
Swainson's Thrush	17
Wood Thrush	9
Gray Catbird	1
Magnolia Warbler	10
Kentucky Warbler	15
Hooded Warbler	19
Worm-eating Warbler	15
Yellow-breasted Chat	6
Ovenbird	14
Painted Bunting	1
Indigo Bunting	8

Table 1.7. Total captures, number and percent of individuals recaptured more than one night after initial capture and more two nights after initial capture.

Species	Total Captures	Recaptures	Percent Recaptured	Recaptured After 48 h	Percent Recaptured after 48 h
Empidonax sp.	35	2	5.7	2	5.71
Gray-cheeked Thrush	58	3	5.2	1	1.72
Swainson's Thrush	323	20	6.2	9	2.79
Wood Thrush	120	26	21.7	15	12.50
Gray Catbird	38	1	2.6	1	2.63
Magnolia Warbler	39	4	10.3	4	10.26
Kentucky Warbler	136	25	18.4	22	16.18
Hooded Warbler	171	42	24.6	30	17.54
Worm-eating Warbler	78	17	21.8	12	15.38
Yellow-breasted Chat	43	3	7.0	2	4.65
Ovenbird	68	19	27.9	14	20.59
Painted Bunting	31	2	6.5	1	3.23
Indigo Bunting	159	5	3.1	4	2.52

Table 1.8. Flight capacity estimates for average individuals of the study species indicating cost of flight (g of fat/h), maximum hours possible based on a single day at the study site, and estimates for maximum hours and distances possible assuming all mass greater than fat free mass is fat.

Species	Flight cost (g/h)[a]	Hours of flight daily gains[b]	Maximum hours of flight[c]	Maximum flight distance (km)[d]
Gray-cheeked Thrush	0.26	n/a	7.62	310
Swainson's Thrush	0.29	2.96	23.02	937
Wood Thrush	0.44	8.29	12.15	495
Gray Catbird	0.33	n/a	10.09	411
Magnolia Warbler	0.08	8.23	12.75	519
Worm-eating Warbler	0.13	4.87	21.82	888
Kentucky Warbler	0.13	n/a	15.87	646
Hooded Warbler	0.10	n/a	23.59	960
Ovenbird	0.18	3.32	17.29	704
Indigo Bunting	0.14	n/a	16.91	688

Table 1.8. (continued)

[a] Based on calculations from Tucker (1974).

[b] Capacity estimates based on 39.8 kJ/g of fat (Nisbet et al. 1963).

[c] Determined by subtracting average mass from average fat-free mass (from Odum in Dunning 1993) and assuming difference is fat.

[d] Assuming average speed of 40.7 km/h for an average Swainson's Thrush (Nisbet et al. 1963).

Table 1.9. Number of sampled individuals and estimated proportion of the population with sufficient fat to fly 1150 km from Los Tuxtlas to Galveston, Texas using fat-free mass (1, from Odum in Dunning 1993) and zero fat score individuals (2) as a base.

Species	# of individuals		% of population	
	1	2	1	2
Empidonax sp.	na	1	na	2.9
Gray-cheeked Thrush	3	3	5.2	5.2
Swainson's Thrush	81	34	25.6	10.7
Wood Thrush	6	6	5.1	5.1
Gray Catbird	1	0	2.6	0.0
Magnolia Warbler	3	2	7.7	5.1
Kentucky Warbler	29	19	22.0	14.4
Hooded Warbler[a]	73	0	42.7	0.0
Worm-eating Warbler	23	13	29.5	16.7
Yellow-breasted Chat	na	1	na	2.3
Ovenbird	10	1	14.7	1.5
Painted Bunting	na	1	na	3.2
Indigo Bunting	28	12	17.8	7.6

Table 1.9. (continued)

[a] The dramatic difference between the two methods may be a result of the substantial difference between the average fat-free masses of the two techniques in a relatively small species (1.32g).

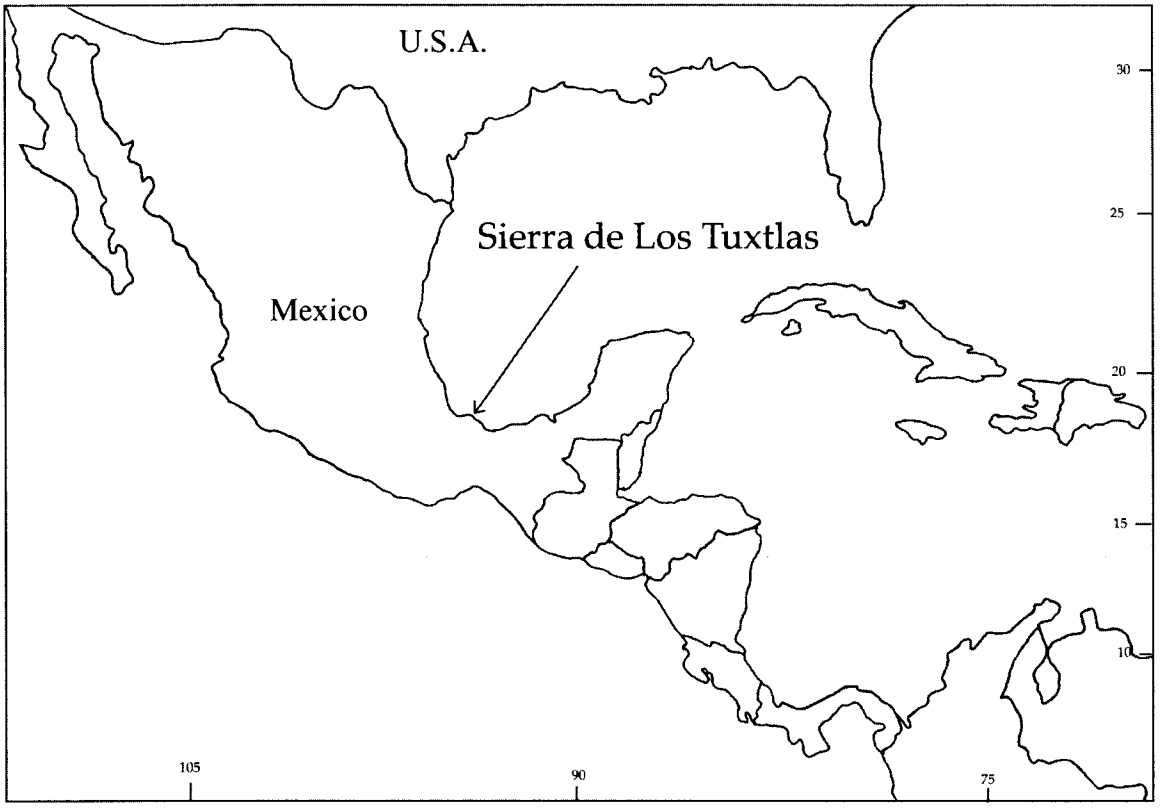

Figure 1.1. Map of Mexico and Central America indicating location of field site.

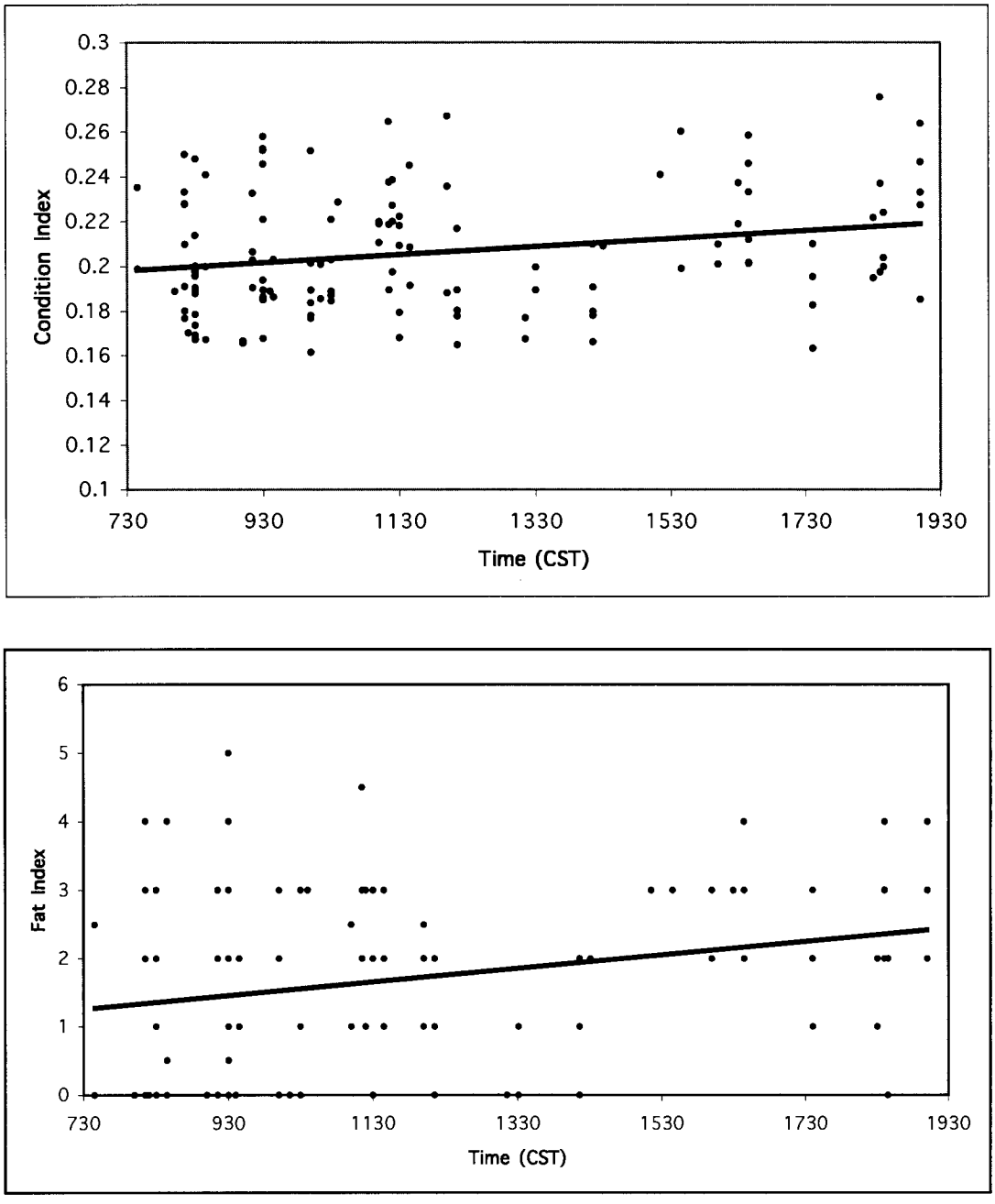

Figure 1.2. Condition and fat indices regressed against time for Kentucky Warblers captured during spring migrations of 2003 and 2004 in the Sierra de Los Tuxtlas, Mexico (Condition: $N = 133$, $r^2 = 0.05$, $P = 0.004$; Fat Index: $N = 133$, $r^2 = 0.065$, $P = 0.003$) with best linear model.

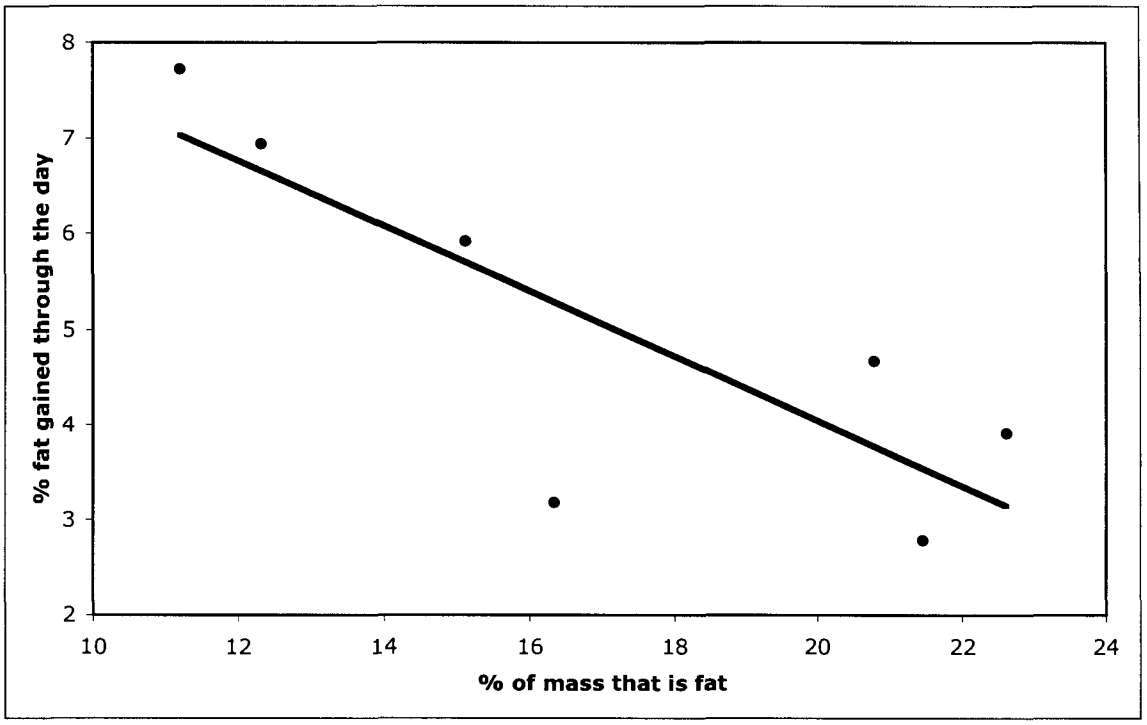

Figure 1.3. Regression of percent of mass carried above fat-free mass (estimated from Odum 1993) vs. estimated percent of mass (based on g of fat from Table 1.5) gained during the day at the Sierra de Los Tuxtlas, Mexico for the seven migrant species showing significant positive increases in body condition (R^2=0.675, P=0.023).

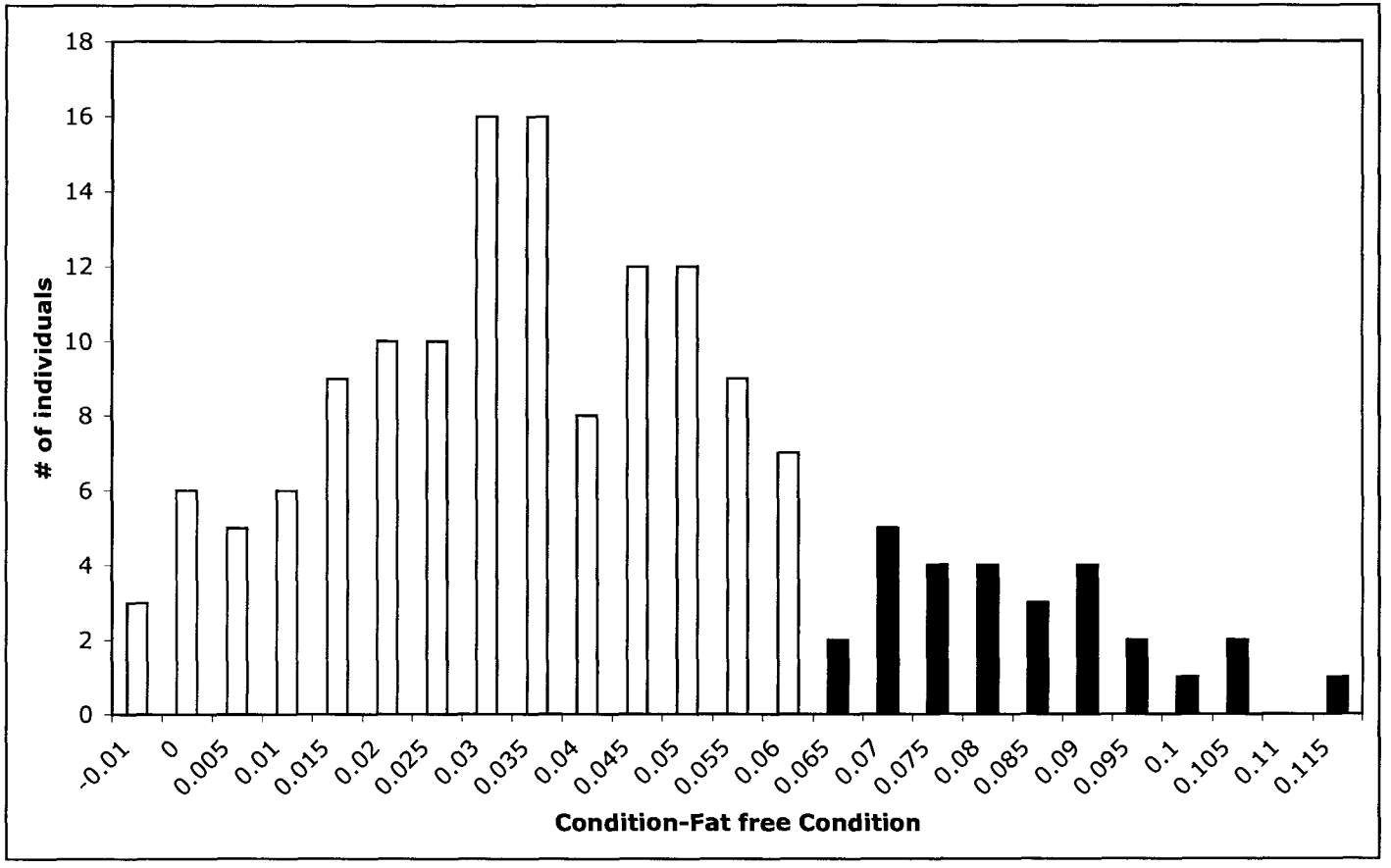

Figure 1.4. Relationship of estimated fat (Condition index – fat free condition) for Indigo Buntings captured in spring at the Sierra de Los Tuxtlas. Those with sufficient fat to complete a flight of 1150 km (the distance from Los Tuxtlas to Galveston, Texas) are shown in black.

Chapter 2: Bird species losses resulting from deforestation in the lowlands of the Sierra de Los Tuxtlas, Veracruz, Mexico*

2.1 Abstract

The Sierra de Los Tuxtlas of southern Veracruz, Mexico is home to the farthest north Neotropical rainforest. This region has been extensively deforested over the past half-century. The Estacion de Biologia Tropical Los Tuxtlas, operated by the Universidad Nacional Autonoma de Mexico, protects a 700 ha tract of lowland forest, which became relatively isolated from other tracts between 1975 and 1985. Forest birds were sampled at the station and surrounding areas using mist nets during eight non-breeding seasons between 1973 and 2004. Using data collected during these efforts I was able to detect local extinctions or declines in 12 species of birds subject to capture in mist nets. Six of the eight species no longer present were captured in 1992-95, but not in 2002-2004. Presence/absence information from netting and observational data suggest that an additional five low-density species have also disappeared since sampling began. The majority of deforestation took place in Los Tuxtlas during the 1970s and early 1980s. This indicates a substantial time lag between the loss of habitat and the apparent extirpation of these species.

2.2 Introduction

Deforestation is one of the main threats to the conservation of biodiversity. Loss of forests and fragmentation of those remaining forests have resulted in the declines or

* Shaw, D. W., K. Winker, P. Escalante, J. Rappole, M. Ramos, R. J. Oehlenschlager and D. Warner. Bird species losses resulting from deforestation in the lowlands of the Sierra de Los Tuxtlas, Veracruz, Mexico. In preparation for submission to Conservation Biology.

local extinction of species at many locations throughout the world (Turner 1996). Perhaps nowhere has this phenomenon been more noticeable than among tropical forests, where a number of studies have documented species losses in numerous taxonomic groups (Zimmerman and Bierregaard 1986, Powell and Powell 1987, Malcolm 1988, Pahl 1988, Becker et al. 1991, Daily and Ehrlich 1995, Brook et al. 2003, Stuart et al. 2004, and others), including birds (Willis 1974, 1979, Leck 1979, Karr 1982, Bierregaard and Lovejoy 1989, Kattan et al. 1994, Robinson 1999, Sodhi et al. 2004). Species losses can occur at the landscape or patch levels and depend greatly on the intensity of the change in forest cover, the distance to and size of other forest fragments, shape and size of the fragment, and other factors (Robbins 1980, Lovejoy et al. 1984, Lovejoy et al 1986, Rolstad 1991, Andrén 1994, Faaborg et al. 1995). Tropical forest species, which often occur in small, low-density populations, may be particularly vulnerable to local extinctions (Tereborgh and Winter 1980, Pimm et al. 1988, Stotz et al. 1996).

Although deforestation and fragmentation can occur over a short period, some time may pass before species begin to disappear from an affected area (Leigh 1975, 1981, Karr 1982, Brooks et al. 1999). Thus, to fully document the impact of deforestation on a rainforest community, a site must be studied for a substantial period of time after habitat alteration occurred. Detailing the process of local population decline and extinction over time provides valuable information about species' abilities to cope with habitat fragmentation.

Most studies of species losses in birds have relied on comparing species richness in different-sized fragments (Willis 1979, Newmark 1991, Blake 1991). This method,

though practical, has the notable disadvantage of comparing among sites, which introduces variability in geography and habitat. Another method has been to compare species composition at a site pre- and post-fragmentation (Willis 1974, Leck 1979, Bierregaard and Lovejoy 1989, Kattan 1994). This second method can demonstrate that local extinctions or declines have occurred, but such studies require the existence of pre-fragmentation survey data, a scarce commodity in much of the world. Experimental fragmentation in the Brazilian Amazon has provided some relevant data (Lovejoy et al. 1986, Bieregaard and Lovejoy 1986, 1989, Ferraz et al. 2003). Other studies documenting avian species loss from Neotropical forest fragments have relied on scattered survey data prior to fragmentation (Willis 1974, Leck 1979, Kattan 1994, Robinson 1999). All of these studies have relied on qualitative visual and audio survey techniques, with multiple observers. These survey techniques can allow cryptic and low-density species to be overlooked (Whitman et al. 1997). Additionally, observer skills and intensity of sampling may vary among surveys. Few studies documenting avian species losses have used a technique with equivalent sensitivity between sample periods.

Mist netting offers the most consistent and quantitative method available to sample birds among years (Rappole et al. 1998). However, mist nets have documented weaknesses; the most relevant is the limited stratum and size of birds they sample (Remsen and Good 1996, Whitman et al. 1997, Rappole et al. 1998). This is particularly noticeable in structurally diverse habitats such as tropical rainforests where probability of detection using mist nets is unknown for most species. Mist net studies in the Neotropics

are therefore biased toward understory, small- to mid-sized passerines. Mist nets, unlike other methods are less prone to observer bias and variability.

The Sierra de Los Tuxtlas of southern Veracruz, Mexico provides a textbook case of deforestation. The small range of volcanic mountains is home to the farthest north Neotropical rainforest (Pennington and Sarukhan 1968). The region has lost more than 90% of its forests in the past century, with the majority of that loss occurring in the lowlands over the past fifty years (Dirzo and Garcia 1992, Rappole et al. 1994, Winker 1996). This study compares eight seasons of mist net sampling from Los Tuxtlas over the course of more than thirty years. This allows us to document the declines and losses of bird species using a consistent technique in an area that has undergone extensive deforestation during a decades-long survey period.

2.3 Site Description and Methods

2.3.1 Site Description

The Sierra de Los Tuxtlas is located in southern Veracruz, Mexico, 90 km southeast of Veracruz city (Fig. 2.1). This range of mountains lies in the northwestern portion of the Isthmus of Tehuantepec and is isolated from the Sierra Madre Oriental by extensive lowlands. Los Tuxtlas encompass approximately 42,000 km^2 and is dominated by Volcan San Martin and Volcan Santa Marta, each reaching more than 1,500 m in elevation. The Gulf of Mexico lies a short distance from the mountains to the north and east. The farthest north Neotropical evergreen rainforest formerly dominated the habitat in the region (Pennington and Sarukhan 1968), but due to deforestation it is now a mosaic with a high percentage of pastureland, fencerows, and isolated trees (Dirzo and Garcia

1992). Andrle (1966) estimated that 50% of the region was forested in 1962, by 1975 Rappole and Warner (1980) estimated a third of the forests still stood, 15% of forests remained in 1986 (Winker et al. 1990, Dirzo and Garcia 1992), and in 1994 only 7-10% of the region was forested (Winker 1996). Remaining forest lies primarily in the highlands, and below 500 m forest is scarce (Rappole et al. 1994, Figs. 2.2, 2.3).

The climate is hot and wet, with a mean annual temperature of 25 C, and annual precipitation is 4,500-4,900 mm, with a short dry season from March-May (Soto and Gama 1997). Canopy heights in the primary forest range from 30-35 m (Ibarra-Manriquez et. al. 1997). Second growth areas generally have variable canopy heights from 3-20 m (pers. obs.).

In 1967 the Universidad Nacional Autonoma de Mexico established the Estacion de Biologia Los Tuxtlas, and protected a 700 ha tract of lowland rainforest (18° 34'30"N, 95° 04'20"W, Dirzo et al. 1997). Over the next decades this site became largely isolated from other tracts of forest (Dirzo and Garcia 1992; Fig. 2.4). The first intensive sampling of birds in the region began in 1973, data from which are included in this study (see Winker 1997).

2.3.2 Field Methods

During the non-breeding seasons 1973-74 and 1974-75 Oehlenschlager, Ramos, Rappole, and Warner conducted the first intensive mist-netting effort in the area. Sites extended through what was then contiguous rainforest from the biological station north and east to the coast (Fig. 2.4). In 1986 Rappole, Ramos, and Winker operated mist nets at the biological station, and Winker and Escalante continued work there from 1992 to 1994. In

2003-04 as part of a study of migrant birds I operated mist nets at the same location as Winker and Escalante's work in the 1990s. All fieldwork occurred during the non-breeding season. Effort was made to equally sample the available forest types throughout the study period (see Winker 1995; Fig. 2.4). Field effort as gauged by net hours varied among years (Table 2.1).

2.3.3 Data Analyses

Only resident species were used in our analyses due to seasonal migration and the high levels of variance in abundance this causes among obligate migrants. Changes in abundance were detected by comparing capture rates (birds per 1000 net hours) from each year of sampling. Species not captured in later sampling efforts and those with apparently declining or increasing rates of capture were selected for more detailed analyses (instead of applying statistical tests across all species). Additionally, presence/absence patterns and observational data were considered to provide insight into changes in abundance in low-density species that did not have sufficient samples for statistical testing. Species were considered for examination for presence/absence if they had not been captured since at least 1986-87. Vagrants, defined as those rarely encountered species whose ranges do not normally include the Sierra de Los Tuxtlas, were excluded (Howell and Webb 1995). Only first-time captures were used in analyses. Simple linear regression was used to detect changes in abundance for selected species (e.g., Fig. 2.5). I looked for newly appearing species using presence/absence netting, observational and specimen data. Daily checklists were used to corroborate mist net data.

Species showing significant declines and those not captured or observed in later sampling periods were categorized by preferred habitat (edge, forest, or semi-open), food preference (fruit/nectar or insects), elevational range, and whether Los Tuxtlas was at the periphery or core of their geographic range (Howell and Webb 1995). These characteristics were used to determine whether certain traits of the species increased their vulnerability to local extirpation.

2.4 Results

During all sampling efforts 165,083 net hours were accumulated, this is equivalent to 37.7 net years if netting with a single net occurred twelve hours per day (Table 2.1). A species accumulation curve for a representative year (1992) with below average net hours (12,605; mean = 20,220) indicates the avifauna was fully sampled during most field seasons (Fig. 2.6). In total, 126 nonmigratory species were captured (Appendix 2.A.).

Seven species showed significant declines during the sampling period: *Phaethornis striilgularis, Xenops minutus, Glyphorhynchus spirurus, Onychorhynchus coronatus, Myobius sulphureipygius, Henicorhina leucosticta,* and *Eucometis penicillata* (Table 2.2). Of these taxa, four were captured throughout the sampling period: *Phaethornis striilgularis, Xenops minutus, Eucometis penicillata,* and *Henicorhina leucosticta. Glyphorhynchus spirurus* was last captured in 1975 an extended netting period, *Onychorhynchus mexicanus* in 1986, and *Myobius sulphureipygius* in 1994, the last season of fall netting. Four other species were captured in substantial numbers during early sampling periods but were not captured in more recent years: *Lepidocolaptes*

souleyetii, Ornithion semiflavum, Leptopogon amaurocephalus, and *Coereba flaveola,* but these species failed to show significant declines in the regression. *Lepidocolaptes souleyetii* was last captured in 1993-94, and the others were last captured in 1994-95. One species, *Hylomanes momotula,* was captured from 1986-1995 but not in the 1970s or in 2002-04. Though there were no captures in the 1970s, one individual was collected on 17 May 1974 a few km northeast of the station. Only two species (*Trogon collaris* and *Xiphorhynchus flavigaster*) increased significantly in abundance.

Presence/absence mist-net capture data for low-density species suggest that an additional 19 taxa have been extirpated during the sample period (Table 2.3). However, we know from observational data that not all of these species are in fact absent. These taxa include rarely captured large and canopy species (i.e., *Micrastur ruficollis, Cotinga amabilis*), mixed/open habitat specialists (i.e., *Thraupis* spp.), a small stream specialist (*Chloroceryle aenea*), and a highland species (*Myadestes unicolor*) that are not prone to capture in mist nets or at our site. Species such as *Tityra inquisitor,* both *Thraupis* tanagers, and others were known to be present on the site or nearby but were not captured in later sampling periods. Four species of hummingbirds are included in Table 4, but due to inconsistent captures or difficulties in field identification we provide no hypothesis regarding their possible extirpation or persistence at the site. However, *Taraba major, Formicarius analis, Grallaria guatimalensis, Elaenia flavogaster,* and *Schiffornis turdinus* likely have been extirpated. Several species were captured only in later sampling periods (Appendix 2.A.) but were observed or collected throughout the

sampling period suggesting there were no additions to the biological station's avifauna during the study.

Based on all available data during the study (netting and observational data), thirteen species of birds appear to have been extirpated from the biological station over the past three decades. This translates into an average loss of 4.2 species per decade or a local loss of 2.3 % of the entire Los Tuxtlas avifauna (561 spp.; Schaldach and Escalante1997), 6.3 % of the resident avifauna (269 spp.; Schaldach and Escalante 1997) and 13.5 % of captured species (126 spp. Appendix 2.A.)

All 17 species showing significant declines or no longer present on the site prefer some degree of forest cover (Table 2.4). Three species are edge specialists: *Ornithion semiflavum, Onychorhynchus mexicanus,* and *Coereba flaveola.* Twelve prefer closed canopy forest: *Phaethornis striilgularis, Hylomanes momotula, Xenops minutus, Glyphorhynchus spirurus, Taraba major, Formicarius analis, Grallaria guatimalensis, Leptopogon amaurocephalus, Myiobius sulphureipygius, Schiffornis turdinus, Henicorhina leucosticta,* and *Eucometis penicillata.* Two species, *Lepidocolaptes souleyetii* and *Elaenia flavogaster,* prefer semi-open or partly cleared forest.

The Sierra de Los Tuxtlas is the northernmost limit of the ranges of 14 of the 17 species showing declines. *Grallaria guatimalensis* and *Henicorhina leucosticta* are the only species with a distribution extending substantially to the north and west of the study site. The field site is well within the elevational limits for all 17 species (Table 2.4).

Trogon collaris and *Xiphorhynchus flavigaster* are the two species that have significantly increased in abundance over the sample period. Both are occurring at the

core of their range, elevational distribution, and prefer forest habitat. *Trogon collaris* is a frugivore, and *Xiphorhynchus flavigaster* is an insectivore.

2.5 Discussion

Although the absence of a species is not a clear indication of extirpation, given the sample effort in this study it is at minimum an indication of decline. If the data accurately reflect reality, species loss from the fragment of forest at the Estacion de Biologia Los Tuxtlas has been continuing since its isolation. Since 1973, 17 species susceptible to capture in mist nets have either become locally extirpated or are showing significant declines in abundance. The total number of losses and declines is undoubtedly higher than presented, because species not regularly captured in mist nets, such as large-bodied and canopy species, were not adequately surveyed in this study. Species known to be extirpated from Los Tuxtlas include *Sarcoramphus papa*, *Harpia harpyja*, and *Ara macao*. Many additional species have also been categorized as endangered or threatened in the Sierra de Los Tuxtlas (see Winker 1997)

The average rate of loss from the station of 4.2 species per decade is somewhat greater than the rate of loss observed at Barro Colorado Island by Robinson (1999) of 3.3 species per decade. My estimate of species loss however includes only those taxa captured in mist nets, whereas Robinson's work included all species detected through observation.

Of the eight species with data sufficient for statistical analysis showing local extirpation, six were lost between 1992 and 2004, suggesting a continuing extirpation of species from the station. As surrounding habitat was lost, Bierregaard and Lovejoy (1988,

1989) found that species richness in remaining fragments increased as individuals displaced from surrounding areas found their way to remaining forest patches. This increased richness was limited by the lifespan of the individual bird (Bierregaard and Lovejoy 1988, 1989). Unlike the studies by Bieerregaard and Lovejoy (1988, 1989), in which forest patches were suddenly and completely isolated, the forest of the Estacion de Biologia Los Tuxtlas was isolated gradually. Since extirpation seems to be continuing, I expect declines and extinctions to continue for some time at the station, even if no further deforestation occurs in the region (Willis 1974, Robinson 1999).

The earliest sampling of our study area took place over a broader geographic area than the later seasons. During the earliest sampling, large tracts of contiguous forest consisting of various micro-habitats dominated the region and were sampled accordingly (Fig. 2.4). This broader expanse of forest likely provided habitat to more species than the current distribution of forest. Essentially two types of forest were present on the landscape after fragmentation: primary forest and acahual (second growth). Our sampling closely tracked the distribution of these lowland forests, though some of the species now apparently gone from the station may persist in other forest patches in the region. I was unable to separate capture data by site for the early sampling periods and therefore all my findings include data from the somewhat larger area from the station east to the coast.

An assessment of possible causes for the loss of these species reveals no definite patterns. In studies of species loss on Barro Colorado Island in Lake Gatun, Panama, maturation of habitat and loss of open areas was shown to be responsible for the decline

in the island's avifauna (Willis 1974, Willis and Eisenmann 1979, Karr 1982). This is unlikely to be the case at Los Tuxtlas. Though there has been a major degradation of surrounding forests, the station has remained primary forest with areas of second growth. Though a loss of tree species has been described (Dirzo and Miranda 1990), the overall structure of the forest appears to have remained fairly stable.

Los Tuxtlas is at the northernmost extent of the range for 14 of the 17 declining or extirpated species mentioned in this study. Terborgh and Winter (1980) proposed that species at the periphery of their range would be more vulnerable to extinction than those at the heart of their distribution. Their hypothesis was supported by Kattan et al (1994) in a study of Andean cloud forest fragments. Though this hypothesis was later refuted by Johnson (1998), we include it here as another possible cause. Los Tuxtlas is at the edge of all species' geographic ranges endemic to Neotropical rainforest. Why then did only these seventeen species show declines? The elevational distribution of each of these species encompasses sea level to 750 m or more (Howell and Webb 1995) and are unlikely to be responsible for the vulnerability of these taxa.

Twelve of 17, or 71%, of the species showing declines or extirpations in this study are insectivores whereas of the total species captured 41% are insectivores. This suggests foraging guild may contribute substantially to a species' sensitivity to disturbance. Elsewhere insectivores have been shown to be particularly vulnerable to severe habitat change (Kattan et al. 1994, Johnson 2003). Large-scale range shifts, resulting from climate change or other factors, was considered as a possible cause for the disappearance of these species from the biological station. However, this hypothesis

seems unlikely for two reasons. First, the loss of species is directly correlated with the fragmentation and loss of forest in the region and the resulting isolation of the 700 ha Estacion de Biologia Tropical Los Tuxtlas. Second, at least some of the species lost from the station appear to have persisted in the southern portion of Los Tuxtlas near Volcan Santa Marta at least into the mid-1990s (Winker pers. com.). If large range shifts were the cause of these losses, species would likely have disappeared region-wide. Region-wide habitat loss seems to be the best explanation for the species loss observed here, but what particular factors of this loss affect each of these species is unknown.

The local extinctions of seven of the 17 species are particularly notable. *Coereba flaveola* is a widely distributed species known to thrive in manipulated habitats such as gardens and forest edges and is a generalist frugivore and nectarivore (Howell and Webb 1995). This is not a species that is expected to decline as a result of forest fragmentation, as both its habitat and food preferences are well suited to survival in a mosaic landscape, and it is known to persist in a fragmented landscape elsewhere in northern Middle America (Johnson 2003). *Ornithion semiflavum* and *Leptopogon amaurocephalus* are both edge specialists, thus limited fragmentation, creating an increase in edges would seem to be beneficial to these species. Though the habitat protected by the station has remained surprisingly static, the intensity of deforestation in Los Tuxtlas as a whole may be too extensive even for these edge specialists. *Lepidocolaptes souleyetii* and *Elaenia flavogaster* prefer open forest and partially cleared areas (Howell and Webb 1995). The habitat surrounding the station during the 1980s and 1990s was dominated by pasture scattered with isolated trees. In the latter field seasons there was a noticeable decline in

the number of isolated trees and fences constructed of living trees (Winker pers. com.). This loss may account for the extirpation of *Lepidocolaptes souleyetii* and *Elaenia flavogaster*. *Glyphorhynchus spirurus* apparently disappeared from the station between the 1970s and 1986, the first of the documented extirpations. The majority of deforestation across the region took place during this period. This previously abundant species disappeared in just over a decade. Interestingly, on the slopes of neighboring Volcan Santa Marta the species was present at least to the 90s and probably still persists there (Winker pers. com.). In Brazil, *Glyphorhynchus spirurus* persisted in experimentally isolated fragments well after isolation (Stouffer and Bierregaard 1995) and the species persists in highly fragmented forest in southern Belize (Johnson 2003). *Hylomanes momotula* was collected but not netted in 1974, was captured in substantial numbers during 1986 and 1992-94 but was absent in the last two seasons of sampling. This pattern is mysterious. This species has an elevational range extending to 1500 m and may persist in the forests of the upper slopes of Volcan San Martin. If so, I speculate that the station may serve as a sink for this species, where habitat is insufficient for a self-sustaining population but may occasionally be colonized by dispersing individuals (see also Winker et al. 1996). Continued sampling may provide more insight into the abundance patterns of this species.

These analyses suggest that the Estacion de Biologia Tropical Los Tuxtlas is of insufficient size to maintain its full, historic complement of bird species. If deforestation region-wide were to accelerate, eliminating other forest refugia, the station alone (700 ha) would be unable to maintain the historical biodiversity of the region or to provide a

source population for restored forest habitats in many of these species. Given the scale of the deforestation in the region, it is surprising that there are not more species showing declines. The overall size of the remaining forests, particularly in the highlands, may be ameliorating the effects of lowland deforestation. However, increasing or continued isolation of the station will probably limit recolonization from elsewhere and a loss of species will likely continue.

2.6 Literature cited

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes With different proportions of suitable habitat: a review. Oikos 71:355-366.

Becker, P., J. S. Moure, and F. J. A. Peralta. 1991. More about euglossine bees in Amazonian forest fragments. Biotropica 23:586-591.

Bierregaard, R. O., and T. E. Lovejoy. 1988. Birds in Amazonian forest fragments: Effects of insularization. Pages 1564-1579 *in* Acta XIX Congressus Internationalis Ornithologici, Ottawa, Canada.

Bierregaard, R. O., and T. E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta Amazonica 19:215-241.

Blake, J. G. 1991. Nested subsets and the distribution of birds in isolated woodlots. Conservation Biology 5:58-86.

Brook, B. W., N. S. Sodhi, and P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424:420-423.

Daily, G. C., and P. R. Ehrlich. 1995. Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. Biodiversity and Conservation 4: 35-55.

Dirzo, R., and M. C. Garcia. 1992. Rates of deforestation in Los Tuxtlas, a Neotropical area in southeast Mexico. Conservation Biology 6:84-90.

Dirzo, R., and A. Miranda. 1990. Contemporary Neotropical defaunation and forest structure, function, and diversity, a sequel to John Tereborgh. Conservation Biology 4:444-447

Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357-380 *in* Ecology and management of Neotropical migratory birds: a synthesis and review of the critical issues. D. M. Finch and T. E. Martin, editors. Oxford University Press, Cambridge, United Kingdom.

Ferraz, G., G. J. Russell, P. C. Stouffer, R. O. Bierregaard, S. L. Pimm, and T. E. Lovejoy. 2003. Rates of Species Loss from Amazonian Forest Fragments. Proceedings of the National Academy of Sciences of the United States of America. 100 (24) 14069-14073.

Howell, S., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York.

Johnson, A. 2003. Migrant stopover ecology and resident resilience after hurricane Iris in a Neotropical bird community. M.S. Thesis. University of Alaska Fairbanks.

Johnson, C. N. 1998. Species extinction and the relationship between distribution and abundance. Nature 394:272-274.

Kattan, G. H., H. Halvarez-Lopez, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology 8:138-146.

Karr, J. R. 1982. Population variability and extinction in a tropical land-bridge island. Ecology 63:1975-1978.

Leck, C. F. 1979. Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. Auk 96:343-352.

Leigh, E. G., Jr. 1975. Population fluctuations, community stability, and environmental variability. *in* Ecology and evolution of communities. M. L. Cody and J. M. Diamond, editors. Belknap Press, Cambridge, Massachusetts.

Leigh, E. G., Jr. 1981. The average lifetime of a population in a varying environment. Journal of Theoretical Biology 90:213-239.

Lovejoy, T. E., J. M. Rankin, R. O. Bierregarrd, Jr., K. S. Brown, Jr., L. H. Emmons, and M. E. Van Der Voort. 1984. Ecosystem decay of Amazon forest remnants. Pages 295-325 *in* Extinctions. M. H. Nitecki, editor. University of Chicago Press, Chicago.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* Conservation biology: The science of scarcity of diversity. M.E. Soule, editor. Sinauer Associates, Sunderland, Massachusetts.

Malcolm, J. R. 1988. Small mammal abundances in isolated and non-isolated primary forest reserves near Manaus, Brazil. Acta Amazonica 18: 67-83.

Nemark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. Conservation Biology 5:67-78.

Pennington, T. D., and J. Sarukhan. 1968. Arboles Tropicales de Mexico. Instituto Nacional de Investigacciones Forestales.

Pimm, S. L., H. H. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757-785.

Powell, A. H., and G. V. N. Powell. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. Biotropica 19: 176-179.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexcio. Pages 353-393 *in* Migrant Birds in the Neotropics: Ecology Behavior, Distribution and Conservation. A. Keast and E. S. Morton, editors. Smithosonian Institution Press, Washington D. C.

Rappole, J. H., K. Winker, and G. V. N. Powell. 1998. Migratory bird habitat use in southern Mexico: mist nets versus point counts. Journal of Field Ornithology 69:635-643.

Remsen, J. V., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113: 381-398.

Robbins, C. S. 1980. Effect of forest fragmentation on breeding bird populations in the piedmont of the mid-Atlantic region. Atlantic Naturalist 33:31-36.

Robinson, W. D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conservation Biology 13:85-97.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biological Journal of the Linnean Society 42:149-163.

Schaldach W. and P. Escalante. 1997. Lista de Aves. Pages 571-573 *in*: Historia Natural de Los Tuxtlas. E. González S., R. Dirzo, and R. Vogt, editors. Universidad Nacional Autonoma de Mexico.

Sodhi, N. S., L. H. Liow, and F. A. Bazzaz. 2004. Avian extinctions from tropical and subtropical forests. Annual Review of Ecology, Evolution and Systematics. 35:323-345.

Soto, M., and L. Gama. 1997. Climas. Pages 7-23 *in* Historia Natural de Los Tuxtlas. E. Soriano G., R. Dirzo and R.C. Vogt, editors. Universidad Nacional Autonoma de Mexico, D.F., Mexico.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago.

Stouffer, P. C. and R. O. Bierregaard. 1995. Effects of forest fragmentation on understory insectivorous birds. Ecology. 76:2429-45.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.

Terborgh, J. 1992. Maintenance of diversity in tropical forests. Biotropica 24:283-292.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119-133 *in* Conservation biology: an evolutionary-ecological perspective. M.E. Soule and B.A. Wilcox, editors. Sinauer Associates, Sunderland Massachusetts.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200-209.

Whitman, A. A., J. M. Hagan III, and N. V. L. Brokaw. 1997. A comparison of two survey techniques used in a subtropical forest. Condor 99:955-965.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44:153-169.

Willis, E. O. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. Papeis Avulsos de Zoologia 33:1-25.

Winker, K. 1995. Habitat selection in woodland Nearctic-Neotropic migrants on the Isthmus of Tehuantepec. I. Autumn migration. Wilson Bulletin 107:26-39.

Winker, K. 1997. Introduction to the birds of Los Tuxtlas. Pages 535-541 *in* Historia Natural de Los Tuxtlas. E. González S., R. Dirzo, and R. Vogt, eds. Universidad Nacional Autonoma de Mexico.

Winker, K., P. Escalante, J. H. Rappole, M. Ramos, R. J. Oehlenschlager and D. W. Warner. 1996. Periodic migration and lowland forest refugia in a sedentary Neotropical bird, Wetmore's bush-tananger. Conservation Biology 11:692-697.

Zimmerman, B. L. and R. O. Bierregaard. 1986. Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. Journal of Biogeography 13:133-143.

Table 2.1. Sample effort and periods during eight nonbreeding seasons across three decades in the Sierra de Los Tuxtlas, Veracruz, Mexico.

Nonbreeding season	Net hours	Sampling period
1) 1973-74	33,976	15 Aug-26 May
2) 1974-75	36,512	7 Aug-29 May
3) 1986-87	4,310	17 Nov-16 Jan
4) 1992-93	12,605	5 Sep-15 Nov
5) 1993-94	41,142	25 Aug-20 May
6) 1994-95	22,509	15 Aug-15 Nov
7) 2002-03	8,395	21 Feb-27 Apr
8) 2003-04	2,312	5 Apr-29 Apr

Table 2.2. Outcomes of regression analyses for 14 species showing changes in abundance and those not detected in the later sampling periods. Those *P*-values presented in bold are significant at $\alpha = 0.05$.

Species	R^2	*F*	*P*	Last captured
Phaethornis striilgularis [c]	0.514	6.337	**0.045**	2002-03
Hylomanes momotula [a]	0.003	0.210	0.890	1994-95
Trogon collaris [b]	0.540	7.041	**0.038**	n/a
Xiphorhynchus flavigaster [b]	0.536	6.941	**0.039**	n/a
Xenops minutus [c]	0.558	7.578	**0.033**	2003-04
Glyphorhynchus spirurus [c,d]	0.557	7.529	**0.034**	1974-75
Lepidocolaptes souleyetii [d]	0.352	3.265	0.121	1992-93
Ornithion semiflavum [d]	0.052	0.327	0.588	1994-95
Leptopogon amaurocephalus [d]	0.319	2.814	0.144	1994-95
Onychorhynchus coronatus [c,d]	0.533	6.861	**0.040**	1986-87
Myiobius sulphureipygius [c,d]	0.629	10.555	**0.019**	1994-95
Henicorhina leucosticta [c,d]	0.529	6.740	**0.041**	2003-04
Coereba flaveola [d]	0.265	2.164	0.192	1994-95
Eucometis penicillata [c]	0.757	18.725	**0.005**	2002-03

[a] Species captured 1986-1995. See text.

[b] Species showing an increase in abundance.

[c] Species showing a significant decline.

[d] Species not captured in later sampling periods.

Table 2.3. Species not captured or observed from 1992-2004, seasons captured (from Appendix), presence on the field site in later sampling periods, and comments.

Species	Seasons Captured	Presence	Comments
Micrastur ruficollis	1	Y	observed
Heliomaster longirostris	1	?	hummingbird
Florisuga mellivora	1	?	hummingbird
Chlorostilibon canivettii	2	?	hummingbird
Hylocharis eliciae	1, 2	?	hummingbird
Chloroceryle aenea	1, 2	Y	small streams
Dryocopus lineatus	2	Y	observed
Synallaxis erythrothorax	2	Y	observed
Taraba major	2	N	forest understory
Formicarius analis	1	N	forest understory
Grallaria guatimalensis	1, 3	N	forest understory
Elaenia flavogaster	1	N	
Tityra inquisitor	1	Y	observed, canopy
Cotinga amabilis	1	?	canopy
Schiffornis turdinus	1	N	forest understory
Myadestes unicolor	1	Y	highlands
Thraupis abbas	1	Y	observed
Thraupis episcopus	2	Y	observed
Molothrus aeneus	1	Y	observed

Table 2.4. Habitat, foraging preference, elevational range, and position within geographical distribution for 19 species of birds at the Estacion de Biologia Los Tuxtlas (from Howell and Webb 1995).

Species	Habitat preference	Foraging guild	Elevational distribution (m)	Geographic distribution
Phaethornis striilgularis	forest	nectarivore	0-1500	periphery
Hylomanes momotula	forest	frugivore	0-1500	periphery
Trogon collaris	forest	frugivore	0-2400	core
Xenops minutus	forest	insectivore	0-1000	periphery
Xiphorhynchus flavigaster	forest	insectivore	0-1500	core
Glyphorhynchus spirurus	forest	insectivore	0-1200	periphery
Lepidocolaptes souleyetii	semi-open	insectivore	0-1500	periphery
*Taraba major**	forest	insectivore	0-1600	periphery
*Formicarius analis**	forest	insectivore	0-750	periphery
*Grallaria guatimalensis**	forest	insectivore	50-3500	core
Ornithion semiflavum	edge	insectivore	0-1500	periphery
*Elaenia flavogaster**	semi-open	frugivore	0-1600	periphery
Leptopogon amaurocephalus	edge	insectivore	0-1300	periphery
Onychorhynchus coronatus	forest	insectivore	0-1200	periphery
Myiobius sulphureipygius	forest	insectivore	0-1000	periphery
*Schiffornis turdinus**	forest	frugivore	0-750	periphery
Henicorhina leucosticta	forest	insectivore	0-1300	core
Coereba flaveola	edge	frugivore	0-1000	periphery
Eucometis penicillata	forest	frugivore	0-750	periphery

* Presence/Absence data suggest species is extirpated.

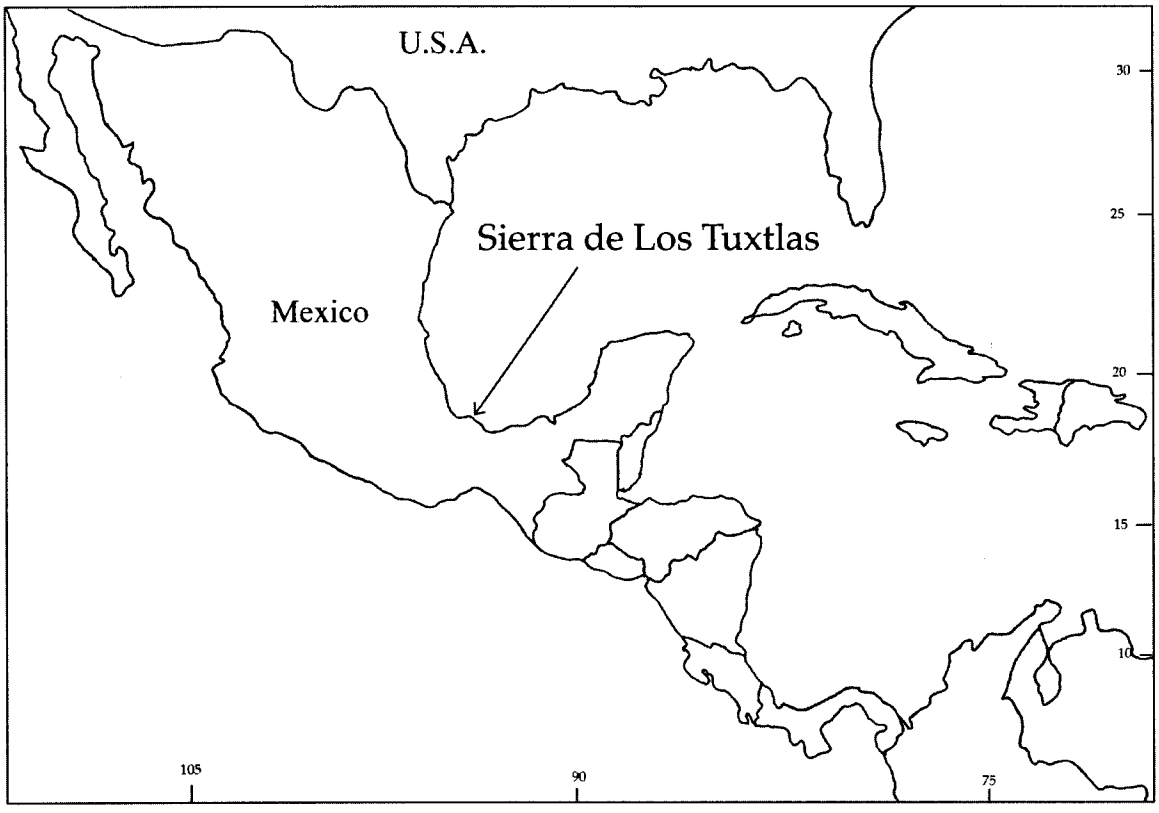

Figure 2.1. Map of Mexico and Central America indicating location of field site.

Figure 2.2. Aerial view of Volcan San Martin, the northernmost volcano in the Sierra de Los Tuxtlas, showing the distribution of forests (dark areas). The field site is indicated by the white arrow (image from GoogleEarth, 2005).

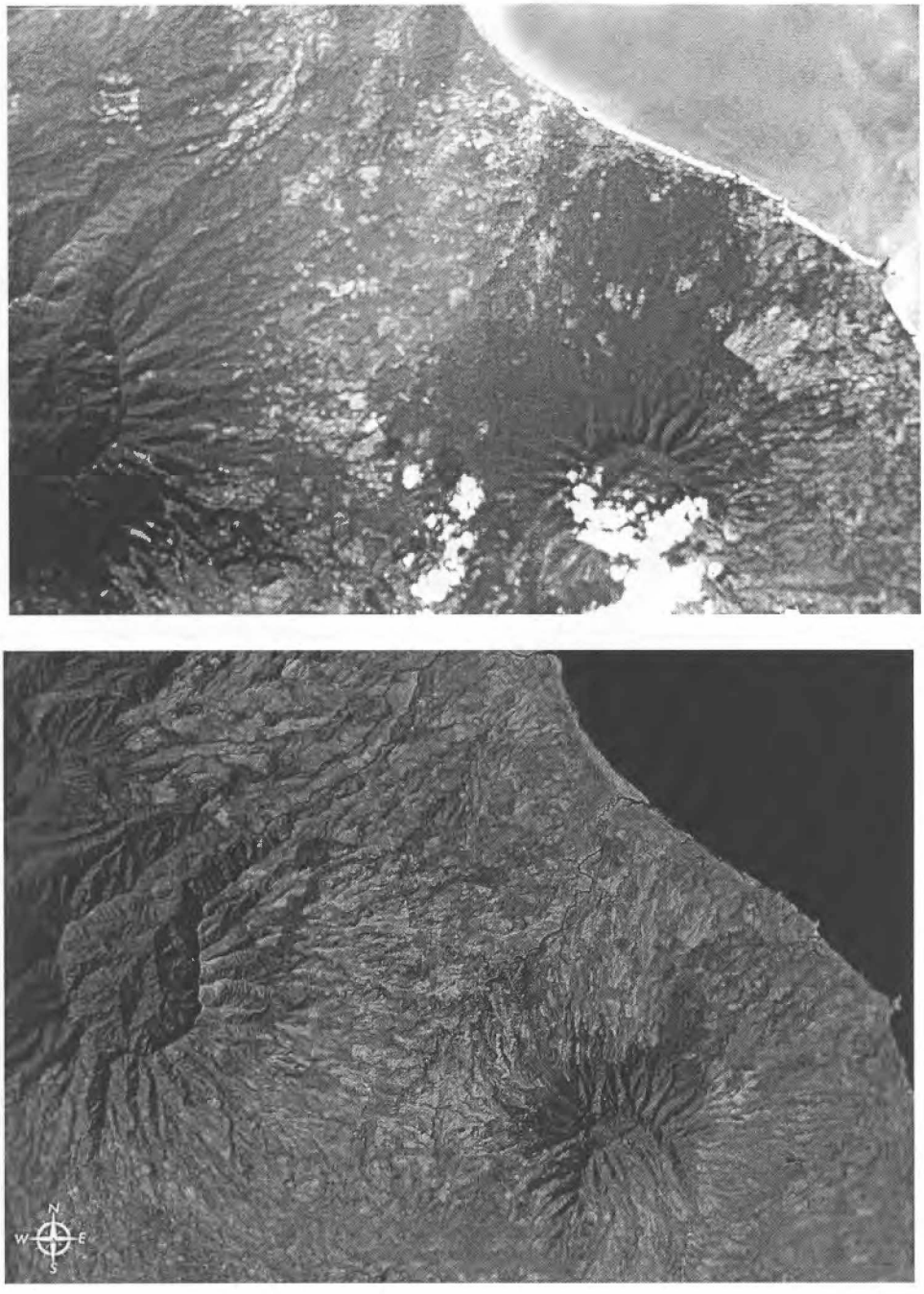

Figure 2.3. Comparative views of Volcan Santa Marta and San Martin Pajapan in the southern Sierra de Los Tuxtlas from 1973 (top; NASA/Skylab) and 2005 (bottom; GoogleEarth) showing extent of deforestation, particularly severe in the lowlands.

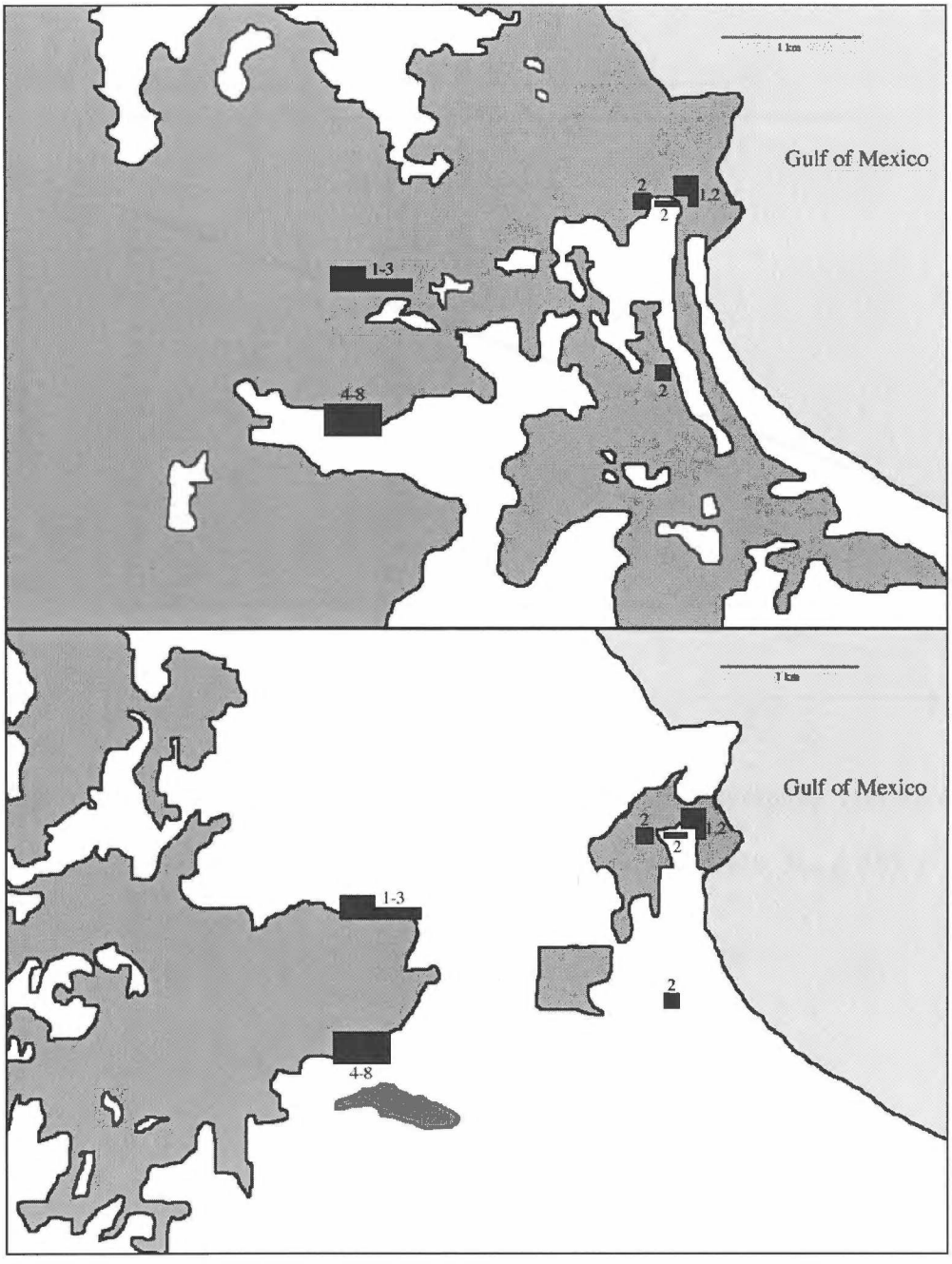

Figure 2.4. Maps of the study area in the northern lowlands of the Sierra de Los Tuxtlas showing a rough outline of all forests types (dark gray areas) in 1979 (top, from Landsat image), present day (bottom, from GoogleEarth), and netting sites (black polygons). Numbers indicate field season(s) site was used (Table 2.1).

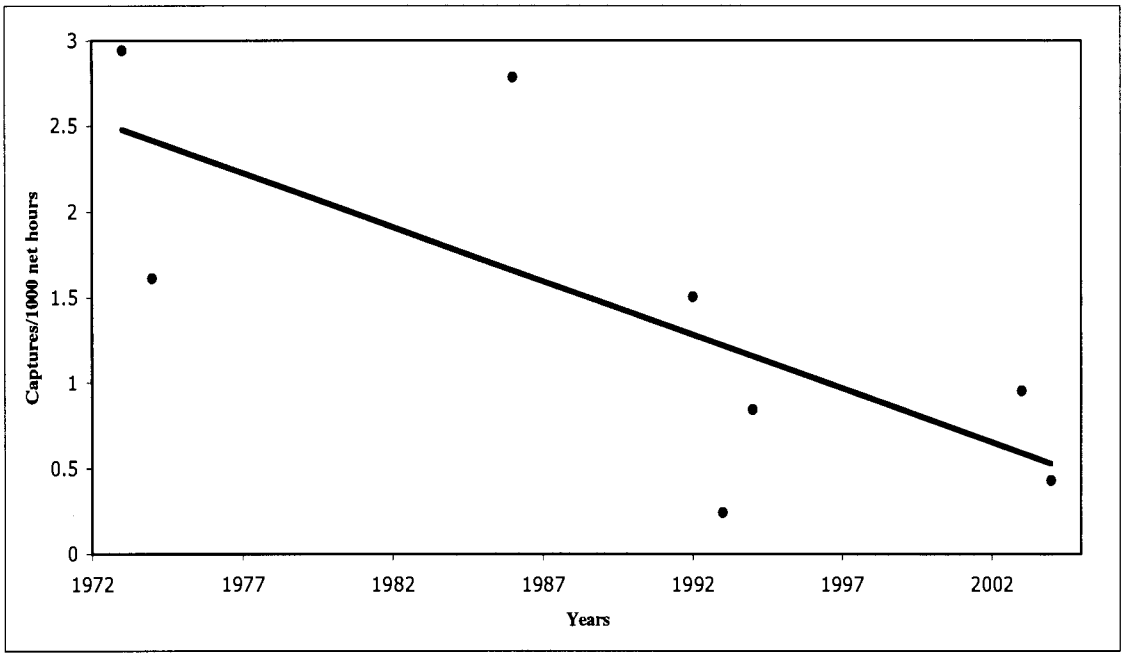

Figure 2.5. Captures per 1000 net hours regressed against sampling year for *Henicorhina leucosticta* in the Sierra de Los Tuxtlas, Mexico ($r^2 = 0.529$, $F = 6.740$, $P = 0.041$).

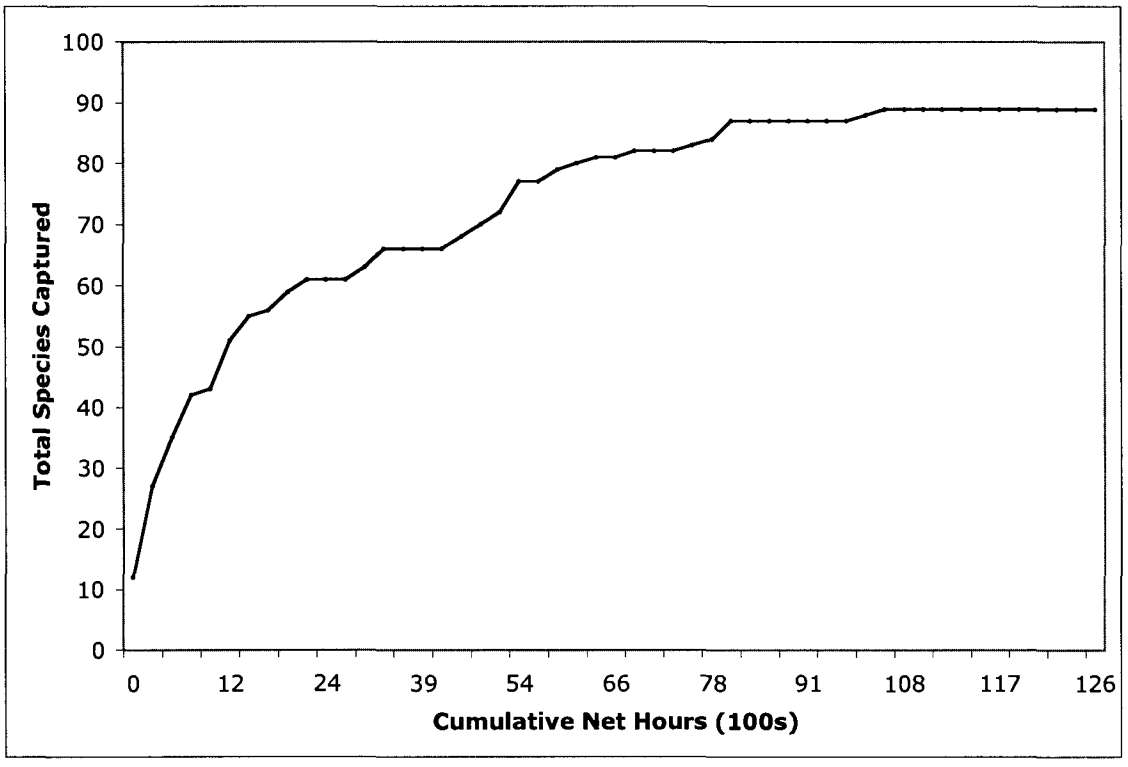

Figure 2.6. Species accumulation curve for a representative year with below average net hours (1992, 12605 net hours).

Appendix 2.A. Species, number of captures (captures per 1000 net hours), and total captures by sampling period.

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	Total
Micrastur ruficollis	3 (0.088)	0	0	0	0	0	0	0	3
Micrastur semitorquatus	0	0	0	0	0	0	1 (0.119)	0	1
Tinamus major	0	0	0	1 (0.079)	0	0	0	0	1
Crypturellus boucardi	0	0	1 (0.232)	0	0	0	0	0	1
Columbina passerina	0	0	0	1 (0.079)	0	0	0	0	1
Columbina talpacoti	0	16 (0.438)	0	3 (0.238)	3 (0.073)	0	0	0	22
Claravis pretiosa	0	3 (0.082)	0	0	0	1 (0.044)	0	0	4
Leptotila verreauxi	0	1 (0.027)	0	12 (0.952)	6 (0.146)	1 (0.044)	0	0	20
Leptotila plumbeiceps	12 (0.353)	5 (0.137)	2 (0.464)	7 (0.555)	5 (0.122)	12 (0.533)	4 (0.476)	1 (0.433)	36
Geotrygon montana	30 (0.883)	6 (0.164)	1 (0.232)	1 (0.079)	3 (0.073)	15 (0.666)	9 (1.072)	0	65
Crotophaga sulicirostris	1 (0.029)	6 (0.164)	0	5 (0.397)	1 (0.024)	1 (0.044)	0	0	14
Piaya cayana	0	2 (0.055)	0	2 (0.159)	1 (0.024)	0	2 (0.238)	0	7
Glaucidium brasilianum	5 (0.147)	7 (0.192)	2 (0.464)	3 (0.238)	1 (0.024)	1 (0.044)	0	0	19
Strix virgata	1 (0.029)	3 (0.082)	1 (0.232)	0	1 (0.024)	0	0	0	6
Nyctidromus albicollis	1 (0.029)	0	0	0	1 (0.024)	2 (0.089)	0	0	4

Appendix 2.A. (continued)

Species	(1)	(2)	(3)
Phaethornis longirostris	186 (5.474)	161 (4.410)	18 (4.176)
Phaethornis striigularis	22 (0.648)	21 (0.575)	1 (0.232)
Heliomaster longirostris	1 (0.029)	0	0
Campylopterus exellens	44 (1.295)	29 (0.794)	7 (1.624)
Campylopterus hemileucurus	83 (2.443)	127 (3.478)	0
Campylopterus zonatus	0	0	1 (0.232)
Florisuga mellivora	4 (0.118)	0	0
Anthracothorax prevostii	0	9 (0.246)	0
Amazilia candida	115 (3.385)	142 (3.889)	2 (0.464)
Amazilia tzacatl	7 (0.206)	31 (0.849)	0
Amazilia yucatanensis	0	0	0
Chlorostilbon canivetti	0	1 (0.027)	0
Colibri thallasinus	0	1 (0.027)	0
Trogon collaris	1 (0.029)	0	1 (0.232)
Trogon massena	0	1 (0.027)	0
Trogon violaceaus	0	0	0

(4)	(5)	(6)	(7)	(8)	Total
68 (5.395)	64 (1.556)	119 (5.287)	22 (2.621)	3 (1.298)	641
6 (0.476)	2 (0.049)	1 (0.044)	3 (0.357)	0	56
0	0	0	0	0	1
31 (2.459)	6 (0.146)	29 (1.288)	9 (1.072)	0	155
48 (3.808)	55 (1.337)	95 (4.221)	15 (1.787)	0	423
0	1 (0.024)	0	0	0	2
0	0	0	0	0	4
0	0	0	2 (0.238)	0	11
25 (1.983)	12 (0.292)	29 (1.288)	23 (2.740)	2 (0.865)	350
1 (0.079)	1 (0.024)	2 (0.089)	1 (0.119)	0	43
2 (0.159)	0	0	0	0	2
0	0	0		0	1
0	0	0	2 (0.238)	0	3
5 (0.397)	2 (0.049)	7 (0.311)	2 (0.238)	1 (0.433)	19
1 (0.079)	0	1 (0.044)	0	0	3
0	0	0	1 (0.119)	0	1

Appendix 2.A. (continued)

Species	(1)	(2)	(3)
Trogon melanocephalus	0	0	0
Pteroglossus torquatus	10 (0.294)	6 (0.164)	0
Hylomanes momotula	0	0	2 (0.464)
Momotus momota	4 (0.118)	3 (0.082)	3 (0.696)
Chloroceryle aenea	2 (0.059)	9 (0.246)	0
Chloroceryle americana	1 (0.029)	0	0
Centurus aurifrons	2 (0.059)	8 (0.219)	0
Centurus pucherani	3 (0.088)	4 (0.110)	0
Piculus rubiginosus	2 (0.059)	4 (0.110)	0
Venilornis fumigatus	15 (0.441)	15 (0.411)	1 (0.232)
Celeus castaneus	7 (0.206)	8 (0.219)	0
Dryocopus lineatus	0	1 (0.027)	0
Lepidocolaptes souleyetii	4 (0.118)	3 (0.082)	1 (0.232)
Xiphorhynchus flavigaster	1 (0.029)	1 (0.027)	7 (1.624)
Sittosomus greisicapillus	39 (1.148)	14 (0.383)	2 (0.464)
Glyphorhynchus spirurius	50 (1.472)	16 (0.438)	0

(4)	(5)	(6)	(7)	(8)	Total
0	0	0	1 (0.119)	0	1
2 (0.159)	2 (0.049)	3 (0.133)	4 (0.476)	0	27
8 (0.635)	7 (0.170)	6 (0.267)	0	0	23
9 (0.714)	2 (0.049)	19 (0.844)	10 (1.191)	1 (0.433)	44
0	0	0	0	0	11
0	0	1 (0.044)	0	0	2
10 (0.793)	2 (0.049)	4 (0.178)	0	1 (0.433)	11
1 (0.079)	0	0	0	0	7
3 (0.238)	0	1 (0.044)	3 (0.357)	0	7
1 (0.079)	1 (0.024)	1 (0.044)	2 (0.238)	1 (0.433)	37
0	0	1 (0.044)	0	0	16
0	0	0	0	0	1
1 (0.079)	0	0	0	0	2
12 (0.952)	9 (0.219)	9 (0.400)	15 (1.787)	6 (2.595)	60
5 (0.397)	4 (0.097)	6 (0.267)	4 (0.476)	0	74
0	0	0	0	0	66

Appendix 2.A. (continued)

Species	(1)	(2)	(3)	(4)
Dendrocolaptes certhia	14 (0.412)	4 (0.110)	2 (0.464)	5 (0.397)
Dendrocincla anabatina	51 (1.501)	22 (0.603)	6 (1.392)	6 (0.476)
Xenops minutus	36 (1.060)	27 (0.739)	1 (0.232)	7 (0.555)
Synallaxis erythrothorax	0	6 (0.164)	0	0
Ramphocaenus melanurus	3 (0.088)	12 (0.329)	2 (0.464)	5 (0.397)
Anabacerthia variegaticeps	0	0	0	5 (0.397)
Automolus ochrolaemus	10 (0.294)	8 (0.219)	2 (0.464)	4 (0.317)
Taraba major	0	1 (0.027)	0	0
Thamnophilus doliatus	0	2 (0.055)	0	5 (0.397)
Formicarius analis	4 (0.118)	0	0	0
Gralaria guatemalensis	1 (0.029)	0	1 (0.232)	0
Ornithion semiflavum	0	7 (0.192)	1 (0.232)	3 (0.238)
Mionectes oleagineus	149 (4.385)	92 (2.520)	36 (8.353)	156 (12.376)
Platyrinchus cancrominus	144 (4.238)	76 (2.082)	14 (3.248)	18 (1.428)
Elaenia flavogaster	4 (0.118)	0	0	0
Onychorhynchus mexicanus	10 (0.294)	3 (0.082)	1 (0.232)	0

(5)	(6)	(7)	(8)	Total
3 (0.073)	2 (0.089)	1 (0.119)	1 (0.433)	14
10 (0.243)	4 (0.178)	4 (0.476)	3 (1.298)	106
5 (0.122)	6 (0.267)	1 (0.119)	1 (0.433)	21
0	0	0	0	6
2 (0.049)	0	4 (0.476)	0	28
5 (0.122)	8 (0.355)	0	0	18
3 (0.073)	7 (0.311)	1 (0.119)	0	35
0	0	0	0	1
5 (0.122)	4 (0.178)	0	0	16
0	0	0	0	4
0	0	0	0	2
0	6 (0.267)	0	0	10
97 (2.358)	140 (6.220)	27 (3.216)	4 (1.730)	701
23 (0.559)	18 (0.800)	21 (2.501)	11 (4.758)	325
0	0	0	0	4
0	0	0	0	14

Appendix 2.A. (continued)

Species	(1)	(2)	(3)
Leptopogon amaurocephalus	20 (0.589)	6 (0.164)	3 (0.696)
Myiopagis viridicata	1 (0.029)	5 (0.137)	0
Tolmomyias sulphurescens	18 (0.530)	12 (0.329)	1 (0.232)
Myiobius sulphureipygius	99 (2.914)	39 (1.068)	1 (0.232)
Myiobius miniatus	0	0	0
Rhynchocyclus brevirostris	63 (1.854)	44 (1.205)	2 (0.464)
Contopus cinereus	0	1 (0.027)	0
Myiarchus crinitus	0	0	0
Myiarchus tuberculifer	1 (0.029)	0	0
Myiarchus tyrannulus	0	11 (0.301)	0
Myiodynastes luteiventris	0	1 (0.027)	0
Attila spadiceus	51 (1.501)	28 (0.767)	5 (1.160)
Pipra mentalis	50 (1.472)	11 (0.301)	18 (4.176)
Megarhynchus pitangua	2 (0.059)	3 (0.082)	0
Pitangus sulphuratus	1 (0.029)	0	0
Myiozetetes similis	2 (0.059)	0	0

(4)	(5)	(6)	(7)	(8)	Total
7 (0.555)	3 (0.073)	3 (0.133)	0	0	45
2 (0.159)	0	0	0	0	8
11 (0.873)	9 (0.219)	6 (0.267)	3 (0.357)	1 (0.433)	61
3 (0.238)	6 (0.146)	2 (0.089)	0	0	17
2 (0.159)	0	0	0	0	2
24 (1.904)	18 (0.438)	36 (1.599)	1 (0.119)	0	188
0	0	0	0	0	1
46 (3.649)	9 (0.219)	11 (0.489)	0	0	66
8 (0.635)	4 (0.097)	5 (0.222)	0	1 (0.433)	19
0	0	0	0	0	11
1 (0.079)	0	0	1 (0.119)	0	3
12 (0.952)	8 (0.194)	7 (0.311)	5 (0.596)	0	116
34 (2.697)	21 (0.510)	22 (0.977)	8 (0.953)	1 (0.433)	165
3 (0.238)	0	1 (0.044)	1 (0.119)	1 (0.433)	6
2 (0.159)	0	0	0	0	3
1 (0.079)	0	0	0	0	3

Appendix 2.A. (continued)

Species	(1)	(2)	(3)
Pachyramphus aglaiae	6 (0.177)	4 (0.110)	0
Tityra inquisitor	1 (0.029)	0	0
Tityra semifasciata	1 (0.029)	0	1 (0.232)
Cotinga amabalis	1 (0.029)	0	0
Schiffornis turdinus	0	1 (0.027)	0
Polioptila caerulea	0	0	0
Polioptila plumbea	1 (0.029)	0	0
Troglodytes aedon	0	0	0
Troglodytes musculus	8 (0.235)	7 (0.192)	1 (0.232)
Henicorhina leucosticta	100 (2.943)	59 (1.616)	10 (2.320)
Thryothorus maculipectus	59 (1.737)	70 (1.917)	6 (1.392)
Hylocharis eliciae	1 (0.029)	1 (0.027)	0
Myadestes unicolor	3 (0.088)	0	0
Catharus mexicanus	0	0	0
Turdus albicollis	0	0	4 (0.928)
Turdus assimilis	7 (0.206)	20 (0.548)	0

(4)	(5)	(6)	(7)	(8)	Total
7 (0.555)	1 (0.024)	1 (0.044)	4 (0.476)	0	13
0	0	0	0	0	1
2 (0.159)	2 (0.049)	0	4 (0.476)	0	10
0	0	0	0	0	1
0	0	0	0	0	1
1 (0.079)	0	0	1 (0.119)	0	2
0	0	0	0	0	1
0	1 (0.024)	2 (0.089)	1 (0.119)	0	4
0	0	0	0	0	16
19 (1.507)	110 (2.674)	19 (0.844)	8 (0.953)	1 (0.433)	167
12 (0.952)	11 (0.267)	12 (0.533)	19 (2.263)	3 (1.298)	192
0	0	0	0	0	2
0	0	0	0	0	3
0	1 (0.024)	0	0	0	1
0	0	0	0	0	4
8 (0.635)	4 (0.097)	8 (0.355)	6 (0.715)	0	26

Appendix 2.A. (continued)

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	Total
Turdus grayi	26 (0.765)	21 (0.575)	7 (1.624)	32 (2.539)	5 (0.122)	22 (0.977)	14 (1.668)	1 (0.433)	81
Vireolanius pulchellus	0	0	0	1 (0.079)	0	0	0	1 (0.433)	2
Hylophilus decurtatus	34 (1.001)	40 (1.096)	0	9 (0.714)	4 (0.097)	2 (0.089)	3 (0.357)	1 (0.433)	93
Hylophilus ochraceiceps	129 (3.797)	54 (1.479)	9 (2.088)	3 (0.238)	4 (0.097)	3 (0.133)	9 (1.072)	2 (0.865)	213
Geothlypis poliocephala	0	0	0	4 (0.317)	0	2 (0.089)	3 (0.357)	0	9
Chamaethlypis poliocephala	0	10 (0.274)	0	0	0	0	0	0	10
Basileuterus culicivorus	0	0	12 (2.784)	43 (3.411)	25 (0.608)	54 (2.399)	8 (0.953)	3 (1.298)	145
Basileuterus rufifrons	4 (0.118)	17 (0.466)	1 (0.232)	3 (0.238)	2 (0.049)	11 (0.489)	2 (0.238)	2 (0.865)	42
Coereba flaveola	2 (0.059)	11 (0.301)	3 (0.696)	2 (0.159)	2 (0.049)	4 (0.178)	0	0	11
Euphonia affinis	0	1 (0.027)	0	0	0	0	0	0	1
Euphonia gouldi	29 (0.854)	24 (0.657)	6 (1.392)	17 (1.349)	19 (0.462)	7 (0.311)	4 (0.476)	1 (0.433)	54
Euphonia hirudinacae	56 (1.648)	47 (1.287)	0	135 (#####)	65 (1.580)	73 (3.243)	50 (5.956)	9 (3.893)	332
Cyanerpes cyanea	9 (0.265)	21 (0.575)	0	6 (0.476)		2 (0.089)	2 (0.238)	0	40
Chlorospingus opthalmicus	2 (0.059)	2 (0.055)	1 (0.232)	80 (6.347)	4 (0.097)	5 (0.222)	2 (0.238)	0	96
Thraupis abbas	1 (0.029)	0	0	0	0	0	0	0	1
Thraupis episcopus	0	3 (0.082)	0	0	0	0	0	0	3

Appendix 2.A. (continued)

Species	(1)	(2)	(3)	(4)
Eucometis penicillata	65 (1.913)	48 (1.315)	2 (0.464)	0
Lanio aurantius	15 (0.441)	14 (0.383)	1 (0.232)	4 (0.317)
Habia fuscicauda	204 (6.004)	90 (2.465)	28 (6.497)	26 (2.063)
Habia rubica	112 (3.296)	78 (2.136)	18 (4.176)	34 (2.697)
Saltator atriceps	1 (0.029)	1 (0.027)	0	0
Saltator maximus	0	7 (0.192)	2 (0.464)	2 (0.159)
Carythraustes poliogaster	7 (0.206)	11 (0.301)	10 (2.320)	6 (0.476)
Cyanocompsa cyanoides	34 (1.001)	21 (0.575)	2 (0.464)	3 (0.238)
Cyanocompsa parellina	19 (0.559)	22 (0.603)	0	13 (1.031)
Arremenops rufivirgatus	1 (0.029)	5 (0.137)	0	5 (0.397)
Volotina jacarins	2 (0.059)	131 (3.588)	0	13 (1.031)
Tiaris olivacea	11 (0.324)	42 (1.150)	4 (0.928)	23 (1.825)
Sporophila torqueola	0	0	0	6 (0.476)
Aimophila rufescens	0	0	0	2 (0.159)
Molothrus aeneus	1 (0.029)	0	0	0
Dives dives	0	0	0	0

(5)	(6)	(7)	(8)	Total
0	1 (0.044)	2 (0.238)	0	118
2 (0.049)	6 (0.267)	0	1 (0.433)	14
12 (0.292)	17 (0.755)	36 (4.288)	11 (4.758)	424
12 (0.292)	29 (1.288)	18 (2.144)	4 (1.730)	305
0	0	0	0	2
3 (0.073)	0	4 (0.476)	0	6
7 (0.170)	11 (0.489)	1 (0.119)	0	53
7 (0.170)	8 (0.355)	4 (0.476)	0	79
11 (0.267)	16 (0.711)	24 (2.859)	0	64
5 (0.122)	3 (0.133)	0	2 (0.865)	16
0	16 (0.711)	0	0	162
5 (0.122)	10 (0.444)	1 (0.119)	1 (0.433)	44
2 (0.049)	39 (1.733)	2 (0.238)	1 (0.433)	50
1 (0.024)	0	0	0	3
0	0	0	0	1
0	0	0	2 (0.865)	2

Appendix 2.A. (continued)

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	Total
Amblycercus holoscierus	0	15 (0.411)	1 (0.232)	5 (0.397)	1 (0.024)	0	1 (0.119)	0	23
Icterus dominicensis	0	0	0	0	0	1 (0.044)	0	0	1
Icterus galbula	0	0	0	11 (0.873)	1 (0.024)	2 (0.089)	0	0	14

GENERAL CONCLUSION

My research into the stopover ecology of migrant birds in the Sierra de Los Tuxtlas has demonstrated that our understanding of passerine migration routes and energetics is not yet sufficient to define the needs of the species in question. Though fat is being deposited through the day by a slight majority of the species present on the site, no average individual of any of the study species is carrying sufficient stores, on average, to cross the Gulf of Mexico from Los Tuxtlas. Surprisingly, this includes species that were previously thought to be exclusively trans-gulf migrants. In addition to providing insight into where and when migrants acquire energetic reserves during stopover, the new information gathered in my study provides another piece of information to help us understand migratory pathways.

The loss of species from the Estacion de Biologia Tropical Los Tuxtlas suggested here is concerning. Seventeen species of birds prone to capture in mist nets have either been extirpated or shown significant declines over the past 30 years, a loss of 2.3% of the historic Los Tuxtlas avifauna, 6.3 % of the resident avifauna and 13.5 % of the captured species. These data, though disturbing, provide important information into the process of species loss from fragmented tropical forest. In the future, this information may be useful in the planning of preserves. It allows us to better understand species losses following deforestation, the importance of habitat preservation, and vulnerability of species. Information that hopefully will aid in preventing continued extirpation of species from the Sierra de Los Tuxtlas and elsewhere.